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PHYLOGENETIC ANALYSIS OF THE BRYOZOAN SUBORDER RHABDOMESINA

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PHYLOGENETIC ANALYSIS OF THE BRYOZOAN SUBORDER RHABDOMESINA

By

Lance Paquette

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ABSTRACT

PHYLOGENETIC ANALYSIS OF THE BRYOZOAN SUBORDER RHABDOMESINA

By

Lance Paquette

The Suborder Rhabdomesina is a group of Paleozoic bryozoans that has been taxonomically problematic when it comes to the evolutionary pattern and relationships within the group. It is not even well understood if it merits subordinal or ordinal rank. No prior phylogenetic attempts have uncovered the evolutionary history of the group. This cladistic study uses genera from many different published sources that have been placed within this order/suborder at any given time. The character list that was used to code each individual genus was developed from a variety of published sources and also some were developed independently during the research and coding process of this study. This was then used to create a data matrix which could be incorporated into a variety of phylogenetic software packages (PAST, PAUP, and a phenetic analysis). The study compared the three different systematic analyses to see which method produced the best tree and also how this tree related to previous taxonomic assessments. The results showed that conventional taxonomy could not be replicated in a cladistic analysis of the suborder/order, with only small percentages of similarity between cladistic and conventional taxonomies. Also, when unplaced or unknown genera were added, the results showed possible convergences between rhabdomesines and other cryptostomes.

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INTRODUCTION

The rhabdomesines are an order or suborder of bryozoans with colonies ranging in size from less than a millimeter (<.5mm) to a few millimeters (up to 7mm) in diameter and are generally slender, cylindrical or radial in cross section, and typically dendroid, branching into different segments with growth. Rhabdomesines are found throughout suites of Paleozoic age marine rocks (Late Silurian-Permian) from a variety of localities around the world, and from a single locality in the Middle Triassic. Their overall morphology has been described in considerable detail in many publications (e.g., Blake 1983, Gorjunova 1985, and Dzik 1992), providing drawings, photographs, SEM images, and generic descriptions.

Only a handful studies have been published on bryozoan cladistics (e.g. Blake and Snyder 1987, Anstey and Pachut 1995), most of which do not deal specifically with rhabdomesines (an exception is Blake and Snyder, 1987), and a debate persists concerning the family-rank taxonomy and systematic of the Suborder Rhabdomesina. This controversy (see Blake 1983, 1987; Gorjunova 1985, 1992; Anstey and Pachut 1995) mainly concerns the status of the suborder within the order, and the number of genera included in the order/suborder along with the number of subfamilies and families to include in the Rhabdomesina, with different sources containing different numbers of each. This situation makes the group an obvious candidate for a cladistic taxonomic reassessment.

The goal of this study is to develop a large enough dataset to resolve the phylogeny of the Suborder Rhabdomesina, and to discover whether or not the rhabdomesines are one distinct, monophyletic suborder of the Cryptostomida, or are a polyphyletic group, composed of more than just one suborder, and how conventional taxonomy relates to the results of this study. Other hypotheses that follow from this primary one are questions concerning ancestry and descent, meaning which clusters of taxa are supported by the results and which characters define any obvious cluster. Do some unplaced genera or those with uncertain affinities belong to the rhabdomesines or are there effects of convergences, reversals, and parallelisms among these unplaced taxa? Finally, do the stratigraphic ages and order on the cladogram have anything to do with possible radiations (Table 5)? These can all be tested by compiling a large data matrix using as many ordered (Wagner) characters as possible, trying to keep unordered or unknown characters to a minimum if not disregarded.

PREVIOUS WORK

Only two cladistic studies (Blake and Snyder 1987, Spearing 1998) have attempted resolving the rhabdomesine suborder using genera as operational taxonomic units (OTUs), and neither has been conclusive with the former using 36 genera and 43 morphological characters with 100 derived states and the latter using 58 genera with 39 characters and 81 derived states. These studies contained a different set of taxa and produced completely different results. Unfortunately, Spearing's (1998) analysis resulted in an unknown number of most parsimonious trees (MPTs), or shortest tree of equal length and produced twelve different consensus trees, most of which had completely unresolved polytomies, meaning that all branches connected directly to the root of the tree. Blake and Snyder's (1987) analysis of rhabdomesines did not sort genera into conventional families and subfamilies as clearly as previously used phenetic methods, only achieving resolution when using small groups, comprised mostly of taxa previously included in the rhabdomesines by Blake (1983) or Gorjunova (1985). This lack of resolution might indicate a non-monophyletic group, or it might reflect widespread convergences between rhabdomesines and trepostomes, as both groups have been used in previous cladistic analyses without achieving resolution between the two orders.

The apparent prevalence of morphological convergences in the suborder, particularly within trepostomes (Blake, 1980; Dzik 1992, 1994) the family has defied internal or external phylogenetic resolution. Anstey and Pachut (1995) hypothesized, using family level OTUs, that the rhabdomesines may be a paraphyletic sister group to the fenestrates, or partly monophyletic (four families) and partly polyphyletic (five families belonging to the fenestrates). Other hypotheses have considered them to be a sister group to the ptilodictyines (Cuffey and Blake 1991) using ordinal level OTUs, while others have found them to be a sister group, in part, to the fenestrates, with only the unilaminate arthrostylids reassigned to the fenestrates (Anstey and Pachut 1995).

The Order Rhabdomesida/Suborder Rhabdomesina has been treated taxonomically in a number of ways. It has been considered by some as a single suborder of the Cryptostomida (Blake 1983; Blake and Snyder 1987; Spearing 1998, see Table 1). Shortly after the revised treatise publication (Blake 1983), Russian paleontologists, particularly Gorjunova (1985), elevated the Rhabdomesida to ordinal status and subdivided it into three distinct suborders: Rhabdomesina, Goldfussitrypina, and Streblotrypina (Gorjunova 1985, see Table 2), each including a number of families and subfamilies. The most recent taxonomy (Gorjunova, 1992, Table 3), retained three suborders, but renamed the Streblotrypina as the Nikiforovellina, with a different number of families and subfamilies contained within each. Finally, an unpublished website created and compiled by Bock (2007) includes the rhabdomesines, and provides a composite taxonomy for them, mostly based on the work of Blake (1983), Taylor (1993) and Gorjunova (1985, 1992), (http://bryozoa.net, Table 4).

Previous cladistic work on the Paleozoic bryozoans is sparse at best. All papers providing taxonomic analyses within the phylum before 1987 did not use cladistics because cladistic software and concepts had not yet been developed or applied to paleontology. However, with improvements in computer software over the past 20 years, around a dozen publications have delved into the phylogenetic relationships among bryozoans' taxa, using updated cladistic software packages, allowing for better, and faster, results. However many studies did not go beyond taxonomic levels lower than the ordinal, and certainly most did not try to establish familial boundaries within the orders.

The first cladistic analysis of the past few decades was by Blake and Snyder (1987). It dealt with the higher taxa of supposed stenolaemates, particularly with the rhabdomesines and trepostomes, looking at whether or not the two groups should be considered separated, or if there was significant convergence between them. The results showed that both cladistic and phenetic analyses supported separation, with the latter presenting a more consistent outcome among three subgroups of the 13 subgroups used in the analysis. However, they did not seem to think that their results required taxonomic revision of either suborder (Blake and Snyder, 1987).

Key 1990 used cladistic analyses to show that a new, mainly Ordivician family, the Bimuroporidae, represented a clade of the trepostomes. The resulting analysis showed that several characters, especially those concerning wall structure, zooidal ontogenetic progression, and growth patterns provided enough proof that four species assigned to the genus *Bimuropora* and four species assigned to the genus *Champlainopora* shared a common ancestor, and therefore the new family Bimuroporidae could be recognized phylogenetically. However, there were some problems, including 19 equally parsimonious trees, resulting in a cladogram with some degree of polytomy, specifically two polytomies among the ingroup. A second analysis was done using only truly informative characters, and its consensus cladogram was discovered to be almost identical to the first, differing in the placement of only one species, making this tree more likely (Key, 1990).

After Blake (1987), Cuffey and Blake (1991) undertook a cladistic analysis of the entire Phylum Bryozoa. They concentrated on purely parsimony-based cladistics, showing the importance of branching sequences within the phylum, and attempting to discover evolutionary order within the phylum. Six orders were used in the study along with a total of 54 characters. Three equally parsimonious trees were found by PAUP and a single one was discovered using a restricted data set comprised only the basal taxa and expanding the data set to 79 characters using soft part characters. The results showed that the cyclostomes and cystoporates are the primitive orders, the trepostomes intermediate, and the three cryptostome groups (which include the rhabdomesines) were the most derived (Cuffey and Blake, 1991). Their results were similar to ones proposed by previous phenetic studies, especially that by Cuffey (1973).

Anstey (1991) did a phylogenetic study of evolution among the major groups, both classes and orders, of Paleozoic bryozoans using 54 two-state and multistate characters. The results showed that the Order Cryptostomida, which has been considered to contain the rhabdomesines, was paraphyletic with respect to the other orders (Ctenostomida, Cyclostomida, and Cystoporida) along with the Class Gymnolaemata. It also showed that the stenolaemates were monophyletic and that the fresh-water bryozoans, the Phylactolaemata, were in between the gymnolaemates and stenolaemates. Finally, it hypothesized that most groups of extant bryozoans were more plesiomorphous than the Paleozoic free-walled stenolaemates, which were the most cohesive derived group (Anstey 1991).

Anstey and Pachut (1995) did initial phylogenetic work on 60 families of Paleozoic stenolaemate bryozoans using 54 (of an initial 58) characters; four were elimated due to their homoplastic nature. The first run was done using codings of the oldest known genus of each family, and produced a tree that showed that the Rhabdomesina, which was composed of 7 families, comprised a paraphyletic stem group to the fenestrates. They also separated the Arthrostylidae into radial and unilaminate groups, to see whether or not the unilaminates forms were actually part of the Rhabdomesina. The first run put the unilaminate forms higher in the tree, including them with the fenestrates, and the radial forms lower, with the other rhabdomesines. The second run used codings based upon nominate or more typical genera of each individual family. The results from this run showed that this run proved to be more congruent with conventional taxonomy. It showed that four families of Rhabdomesina form a monophyletic group which are considered to be a sister group to the Fenestrata. However, the two arthrostylid groups along with the hyphasmoporids were more closely linked to the fenestrates.

Todd's (2000) study on ctenostomes, an encrusting group of bryozoans, provided some criticism of previous phylogenetic studies on bryozoans, mostly those by Anstey (1990), Cuffey and Blake (1991), and Anstey and Pachut (1995). Todd stated that the first and third studies lacked available data matrices and contains numerous insufficiencies in their coding schemes, due to poorly defined and presumeably convergent characters. Todd blamed these problems on the use of higher taxonomic levels for phylogenetic analyses. However, his character lists, used to develop cladograms for both major bryozoan clades and for his species level analysis of ctenostomes, appear to exhibit prevalant homoplasy and both data matrices appear to have a lot of unknown material. As a result his analyses have similar problems to other published cladistic analyses.

In recent literature, some studies have shifted to cladistic analyses at lower taxonomic ranks, specifically those that involve species evolution within a particular genus (Anstey and Pachut 2002, 2004, and 2007). Anstey and Pachut's (2004) study of the species within the genus *Peronopora* includes in-depth cladistic, phenetic, stratophenetic, and typological analyses, and compared the methods used to recognize species within a genus of bryozoans. Pachut and Anstey (2007) showed the correlation between cladistic branching order and stratigraphic occurrences of the species within *Peronopora*. There has been a range of cladistic analyses through the past 20 years, resulting in a variety of conclusions regarding Paleozoic bryozoans.

The challenges for this study revolve around the adequacy of the data and the selection and numbers of genera and morphological characters used. The previous studies that dealt with rhabdomesines did not use enough characters for the number of genera put into the analyses. Although the input of a stratigraphic character into the analyses by Spearing (1998) provided some resolution, breaking up the polytomic structure to some degree, that analysis still lacked adequate phylogenetic resolution. This study will not use stratigraphic data as a cladistic character, unlike Spearing. I will use stratigraphy only for inputting genera in the software in stratigraphic order based on stages in the current International Stratigraphic Chart (http://stratigraphy.org). This study will rely completely on morphological data, some from previous papers, and some characters independently developed, with a 2:1 ratio of characters compared to the number of OTUs to produce a better resolved phylogeny. This study focuses on providing a thorough sampling and taxonomic understanding of a particular suborder that has not, as of yet, been fully understood.

METHODS

Testing whether rhabdomesines are an entire order or rather a few suborders comprised of smaller families requires the use of several computer programs. These include PAUP, PAST, Treeview X, and Corel Draw X3; however PAUP (Swofford 2007) is the preferred choice due to its prevalence in recent literature. The Phylogenetic Analysis Using Parsimony (or PAUP) version 4.0.10b was developed and updated for use in phylogenetic studies, using both morphologic and genetic data. PAlaeontological STatistics (PAST) is a freeware program that can graph, plot, model, and do statistical and parsimony analyses on different kinds of paleontological data, including morphological. Treeview X is a useful program for close examination and better presentation of the trees that PAUP generates. The reason for using a variety of programs is to explore the validity of the trees produced by the programs and tests for which program presents the “best” cladogram. The heuristic search algorithm is used in this study, by both PAUP and PAST. Heuristic searches do not exhaustively find all the possible shortest trees, but require far less computer random access memory (RAM) than an exhaustive or branch-and-bound algorithm.

This is important due to the large size of the data set in this study. Most of the runs were done in PAUP, due to its prevalence in the literature, but PAST was used first because: 1) It isn’t command line driven, making it more user friendly; 2) Trees are created within the program and are better formatted than in PAUP; and 3) It was used as a proxy to see if the PAUP tree(s) could come close to the output of PAST and to see if both programs came up with a similar tree using the same stipulations to see how effective heuristic methods can be. Also, a phenetic cluster analysis was done to see how well it might reflect either conventional or cladistic taxonomy. The addition sequence, or stepwise addition, is what connects taxa to the developing tree until all taxa are connected.

The sequence used for all cases was ASIS, which means that taxa are added in the same order as they are in the data matrix, which was ascending stratigraphic order (old-young), which might possibly assist heuristic searches in finding optimal trees. Because stepwise-addition algorithms generally don’t find optimal trees unless the coded characters lack significant homoplasy, another algorithm, called branch-swapping, is often used to improve the initial stepwise estimate by performing rearrangements that are predefined in order to find a shorter, and perhaps better, tree. The branch-swapping algorithm used for all of the runs of the data is tree bisection-reconnection (TBR), in which the tree is bisected along a branch, yielding two subtrees.

These are then reconnected by joining pairs of branches from each subtree, with all possible bisections and pairwise additions evaluated. The reconstruction of characters at internal (ancestral) nodes is done using character-state optimization, and this is done to minimize the total amount of change of a single character for a given tree. This means that there should be one optimal place for a character to be assigned for a given node; however more than one optimal place may exist for a given tree. This is when an optimality criterion can be used, DELTRAN, which is delayed transformation, meaning character evolution takes place higher in the tree, rather than towards the root, which is called ACCTRAN.

Finally, the steepest descent option was implemented because in this way, the round of tree searching is not abandoned when a shorter tree is found, but continues until all the trees from the previous round have been examined. The problem is that heuristic, branch-swapping methods have to be used due to the number of OTUs incorporated in the study, and even the same program will vary in the number of trees created during individual runs because the output depends on even slight variations in the input parameters entered before the run, which were held constant throughout in all the runs executed for this study.

The characters used in this study are derived from examining published thin sections, SEM photographs, or drawings of thin sections from all of the genera that are included in this study. The character states used to indicate both ancestral/primitive (coded with a "0") and derived (1, 2, 3, etc.) can be in either nominal or ordinal form. All of the characters used were considered ordered (or Wagner) which means if a character in a particular genus goes from state 1 to state 4, it must go through a linear evolutionary progression from state 1-2-3-4, without skipping any states in the process or evolutionary line. The use of Wagner characters makes it easier for both PAUP and PAST to run faster, using fewer assumptions.

The search for nominal or ordinal state characters describing Paleozoic stenolaemates has resulted in 19 publications over the last 37 years: [Anstey & Perry (1970, 1973); Corneliussen & Perry (1973); McKinney (1977, 2000); Anstey (1978); Prezbindowski & Anstey (1978); Pachut & Anstey (1984); Blake & Snyder (1987); Hickey (1988); Anstey (1990); Key (1990); Cuffey & Blake (1991); Hageman (1991); Pachut, Anstey & Horowitz (1994); (Anstey & Pachut 1995 (Appendix A; Appendix B); Spearing (1998); Tang & Cuffey (1998); Taylor & Weedon (2000)] as well as several new characters developed by R. Anstey (personal communication). A combination all of these characters has been incorporated into an overall list of 317 characters with 701 derived states.

The outgroup used for all of the runs was the genus *Wolinella* (Dzik 1981), due to the number of primitive states coded for it along with the fact that it was older (Dapingian) than all the genera used in the study except one used as a second outgroup, *Goryunovia* (Taylor and Rozhnov 1996), which had slighty more derived states despite being stratigraphically older (Floian) by a few million years. All genera (OTUs) included in the ingroup have been put in the rhabdomesines at one time or another, some are still included, some have been removed or have been placed back in, and some genera included in the study are unplaced within the Cryptostomida or have unknown affinities.

The point of including these unknown genera is to see if they indeed belong within the rhabdomesine suborder. They include all those in the 1983 treatise on bryozoans (Blake 1983), some from both Gorjunova (1985, 1992) publications, and the rest from other literature (see References for Genera for the complete list).

The coding of morphological characters for each of the genera relied heavily upon the type species of each genus along with its original description where possible. When that was not available, another species within the genus was used as a substitute. In some cases only silicified remains were illustrated, and the photographs usually did not show any internal structure. In these cases the type species of a morphologically similar genus was used in 3 or 4 instances in order to provide proxy character states. However, and for most of the genera the type species was used. The Bryozoa Homepage website (http://bryozoa.net) states that there are 83 genera in the Suborder Rhabdomesina, 8 in the Suborder Goldfussitrypina, and 7 in the Suborder Streblotrypina for a total of 98 genera.

However, that number is skewed due to the fact that some genera have been multipley assigned into families within the suborders, making the actual number 92 of the 100 total genera taken from all of the papers used for this study. However the unknown affinity genera (see Table 1) were left out of most of the runs to narrow the running time for the software and to establish an initial tree lacking these possibly convergent taxa. Because three genera were not available for coding, the number of genera used in these runs was 89. Also, of the 317 characters described in the character list, only 275 applied to the non-fenestrates, and 42 were applicable only to unilaminate fenestrates. Other characters were excluded because of lack of apparent evolutionary change (characters never changing state from genus to genus, i.e. always 0), or characters that only appeared derived in a single genus (or autapomorphies; Table 2). This resulted in a final count of 89 genera and 198 characters.

The runs were done in PAST first, as stated previously, until a single MPT was found that was shorter than any other and had a relatively high ensemble CI (consistency index, which indicates the consistency of character state transformations with the structure of the tree). Next, a Q-mode cluster analysis was done to show the phenetic relationship among the genera included in the study. Finally, PAUP runs were done using the same stipulations as those in PAST with the exception that due to limited memory, the number of trees that would be held in memory at any one time during any heuristic search was 100. The difference between the PAST and PAUP runs are described below.

Table 1: Genera with controversial/unknown placement, or aberrant growth forms. Bock (2007) was used to show possible placement of genera.

Genus Name	**Order, Family**
Hayasakopora	Trepostomatida, girtyporid
Hyalotechus	Trepostomatida, unplaced
Idioclema	Trepostomatida, eridotrypellid
Pesnastylus	Fenestrida, phylloporinid
Syringoclemis	Trepostomatida, girtyporid
Maychellina	Trepostomatida, maychellinid
Kielcepora	Cryptostomida, kielceporid
Ojlepora	Cryptostomida, kielceporid
Rhombocladia	Fenestrida, phylloporinid
Streblocladia	Rhabdomesida, rhabdomesid
Strebloplax	Rhabdomesida, rhabdomesid

RESULTS

The initial results were done in PAST using the heuristic search algorithm with the TBR option and Wagner optimization with zero reorderings. Starting with zero, the number of reordering was increased in increments of 5, up until 50. This was because after 50, there were no clear differences between trees with higher number of reordering. Also, in every run in PAST, FADs (First Appearance Datum) and LADs (Last Appearance Datum) were put in the first two columns in order to calculate stratigraphic consistency indices. The resulting cladogram that was the shortest and had the highest ensemble CI that PAST could produce within both its limitations and those of the computer used in the study is displayed in Figure 1 and the tree statistics were the following: 445700 trees were evaluated, 1 MPT with a length of 2354 with an ensemble CI of 0.1786, which is relatively low for a MPT, indicating the degree of homoplasy is relatively high.

Table 2: Characters eliminated from final runs of PAST and PAUP due to the fact that these characters are autapomorphies, only occurring in a single genus. Character number corresponds to data matrix in Appendix B.

Characters Eliminated	**Character Type**
Char. 80	Budding
Char. 96	Basal Zooecium
Char. 104	Monilae
Char. 121	Mesozooecia
Char. 132	Cystopores
Char. 170	Interzooecial pores
Char. 171	Interzooecial pores
Char. 172	Interzooecial passage
Char. 243	Pustules
Char. 250	Interzooecial spines
Char. 310	Allozooecia

Further runs were implemented in PAST, using multiples of 10 for the number of reordering above 20, but no significant difference developed in any of the trees calculated. As a parallel to cladistic analyses, a phenetic analysis of both taxa and characters was carried out in PAST. Two different cluster analyses were done, Q-mode and R-mode clustering. In Q-mode analyses, the distributions of variables, in this case morphological characters, are used to group together taxa with similar morphologies. R-mode analysis uses the same data matrix as Q-mode, except it is transposed, meaning that the columns are now the taxa, rather than the characters.

This is done to identify covarying clusters of variates, including characters with perfect similarity to one another, and will cluster them together. The results of these analyses can be seen in Fig. 2 and Fig. 3. The main reason R-mode clustering was done was to see if there were any redundant characters in order to eliminate them from the PAUP run, which in this case were four (characters 215, 228, 231, and 263). These were then removed from the data matrix (Appendix B). Six other characters were also discovered to be redundant, but these were kept because they represented phylogenetically informative states important in conventional taxonomy.

PAUP was then used to see if it could find a similar tree, if not a shorter one. The output from PAUP took priority over that from PAST, because of its ability to show tables and diagrams displaying individual character statistics (CI, RI, or retention index, and RC, rescaled consistency index) which was used in order to show support for clusters generated in individual runs by PAUP. The resulting run using the same data matrix with 89 genera and 189 characters resulted in 12 MPTs that were 2303 steps in length, much shorter than the trees calculated in PAST; however the larger number of equally parsimonious trees did not resolve the situation. Consensus trees were calculated in PAUP in order to see which groups of taxa appeared in all of the rival trees (strict) and to see which groups appeared on a pre-specified percentage of all the trees (majority-rule). The strict consensus trees can be seen in Fig. 4. Examination of both consensus trees shows that they are identical, with the same set of four polytomies in each.

To try to reduce the amount of homoplasy, all of the characters were reweighted using the maximum, minimum, and mean values of the RC, CI, and RI of all 12 trees. The results showed that the reweighting reduced the number of MPTs, most of the reweighted runs resulted in a single parsimonious tree; however despite getting to a single MPT, the structure of the trees became more pectinate or ladder-like. The best results were found using the minimum values for the CI, RI, and RC (Figs. 6, 7, and 8), meaning that these trees were the shortest and had the most balanced structure. From there, the two that had the highest degree of balanced clustering were the RC and CI trees, and the CI was chosen as the best overall tree because it contained more clusters and was less pectinate in overall structure.

The next step was to see which characters defined the clusters presented on the tree. This was done using the apomorphy list in PAUP that shows at any given node what characters are plotted there, the transformations and the character's individual CIs. The characters that were most informative were characters with a CI of 1, therefore any internal node that contained a character with a CI of 1 was therefore defined by that character. The nodes in Table 8 represent clusters in Fig. 12 and list any character that appears at that node and the CI for each character, looking specifically at those characters with a CI equal to 1.

Fig 1: Output from PAST with 20 reorderings, a single MPT with branch length 2354.

```
/------------------------------------------------------------ Wolinella
+------------------------------------------------------------ Goryunovia
|                                         /--- Cuneatopora
|                                        /91/-- Helopora
|                                        92 90-- Moyerella
|                                       /93\----- Osburnostylus
|                                      94 \------ Ulrichostylus
|              /---------------------------95\-------- Sceptropora
|              |                       \--------- Arthroclema
|              |                           /-- Nematotrypa
|              |                            96-- Cyclophaenopora
|              |                          /97--- Clausotrypa
|              |                         98----- Tebitopora
|              |                        /99------ Nemataxis
|              |                       100-------- Neorhombopora
|              |          /------------102     /-- Europora
|              |          |            \----101-- Nicklesopora
|              |          |                 /-- Archaeomeson
|              |          |                 103-- Coelotubulipora
|              |          |                104--- Mediaporina
|              |          |          /---105----- Promediapora
|              |          |          |      /-- Acanthoclema
|              |          |          |     106-- Nikiforovella
|              |          |          |    108/-- Bactropora
|              |          |          |  109107-- Streblotrypella
|              |          |         116    |\----- Pinegopora
|              |          |         || 111  /-- Pamirella
|              |          |         ||112 \-110-- Primorella
|              |          |         || |\-------- Linotaxis
|              |          |        117115     /-- K.Klaucena
|              |          |        | | |   113-- Mediapora
|              |          |       118 | \---114--- K.Spira
|              |         140       | | \----------- Antonoclema
|              |         ||    120 \------------- Nudymiella
|              |         ||    ||          /-- Veroclema
|              |         ||   121\-----------119-- Denmeadopora
|              |         ||   | \---------------- Maychella
|              |         ||  123             /-- NewGenus
|            157          || 124\-------------122-- Uralotrypa
|            | |         || | \------------------- Euthyrhombopora
|            | |         || |          /-------- Trematella
|            | |         || |          | /------ Rhomboporella
|            | |         || |        129 |  /-- Rhabdomeson
|            | |         ||137          |128 125-- Ascopora
176           | |         141| ||          | |126--- Silenella
|            | |       | || ||          | 127----- Pseudorhabdomeson
|            | |       | || ||          |  /----- Saffordotaxis
|            | |       | || |\----------136 132 /--- Artchedella
|            | |       | || |           | |131/-- Shishoviclema
|            | |       | |139           |133 130-- Pictatella
|            | |       | | |            || \------ Rhombopora
|            | |      144 | |           135    /-- Megacanthopora
|            | |      | | | |            \---134-- Lutulentus
|            | |      | | | |                /-- Bigeyella
|            | |      | | | \-----------------138-- Megacanthoporina
```

Fig 1 cont:

```
|          159 |       | | \------------------------- Goldfussitrypa
|           || |    146 |                  /-- Orthopora
|           || |    || |                142-- Heloclema
|           || |    || \--------------------143--- Paranicklesopora
|           || |    ||                  /-- Nemacanthopora
|           || |   151\-----------------------145-- Permoheloclema
|           || |   | |                  /-- Ottoseetaxis
|           || |   | |                /147-- Rozanovia
|           || |  152 |                 | /-- Pseudoascopora
|         160| |   || \---------------------150148-- Ascoporella
|          | || |  153|                149--- Lanopora
|          | || |  | |\------------------------------ Kielanopora
|          | || | 154 \-------------------------------- Hexites
|          | || |155\--------------------------------- Tropidopora
|          | ||156 \----------------------------------- Nematopora
|          | ||  \------------------------------------ Nematoporella
|        164 ||                          /-- Arthrostyloecia
|        | | |\----------------------------------158-- Arthrostylus
|        | | \---------------------------------------- Arthrotrypa
|        | |                         /-- Heminematopora
|       165 |                           161-- Hemiulrichostylus
|       || |                        162--- Arcanopora
|      166| \-----------------------------------163----- Hyphasmopora
|      | |\------------------------------------------- Mitoclema
|     168 \---------------------------------------------- Matsutrypa
|      ||                             /-- Mongoloclema
|      |\------------------------------------------167-- Pseudonematopora
|    171                                /-- S.Streblotrypa
|    | |                             169-- Ogbinopora
|   172 \------------------------------------------170--- S.Streblascopora
|  173\---------------------------------------------------- Petaloporella
|174 \---------------------------------------------------- Nemataxidra
175\------------------------------------------------------- Ipmorella
 \------------------------------------------------------ Vidronovella
```

To try to see how stratigraphy is correlated with cladistic output, the stage used in Fig. 5 was compared to the reweighted CI tree to see how closely they relate to each other. Finally, the encrusting group (*Rhombocladia, Streblocladia,* and *Strebloplax*), was analyzed to determine whether or not they are rhabdomesines and where they fit on the cladogram. These results are shown in Fig. 9. Also included in this run were the unplaced genera or those with unknown affinities. The reason to include them now instead of in the beginning was to see how the most parsimonious tree (the reweighted minimum CI tree) was affected by the inclusion of these taxa and where in the tree the taxa were placed. This was to see if the taxa were basal or derived, or fit into already established clusters, and if their positioning leads to any changes in taxonomy.

A new data matrix was inputted into a text file that contained all of the OTUs coded for this study. Then the notepad file was exported into PAUP and another heuristic search was done using the same parameters as mentioned before. This run resulted in eight MPTs, fewer than before; however the tree was much longer, 2649 steps in length. The resulting strict consensus tree (Fig. 9), and the majority-rule consensus tree (Fig. 10), indicate where the new OTUs cluster. To try to alleviate the number of MPTs discovered, another reweighting session was implemented; again using the minimum value of the CIs, resulting in three most parsimonious trees, with a consensus tree shown in Fig. 11.

The minimum values of the RI and RC were also used in reweighting characters to try to reduce the number of MPTs, but these only resulted in more, 4 and 6 respectively. Lastly, to see which clusters were supported, a phylogram (which portrays branch-lengths to scale based upon amount of character change along the branch), was developed in PAUP to try to tell where good clusters occur (nodes with a CI of 1 at their roots) and what characters are at the base of these clusters. Fig. 10 shows the phylogram created in PAUP, along with the nodes numbered for convenience. Also, a table was created (Table 8), using the apomorphy list, to show where a particular character changed, its CI, and what state the character changed to (e.g. 0-1, 1-2, 0-2). Table 8 only includes character state changes at the base of four prominent clades.

Of particular interest were those characters with CIs of 1, which are the most parsimoniously informative characters and clusters that were supported by these were given priority for support. The four prominent clades have most of the nodes that can be read easily off of the phylogram. The phylogram itself is hard to read due to the nature of PAUPs output. The phylogram shows that the longest branches are those leading to terminal taxa, which is most likely related to the use of the DELTRAN optimization.

The use of ACCTRAN hypothetically would optimize more character states lower in the tree; however when the ACCTRAN optimization was implemented, the structure of the phylogram was unchanged. The lack of the appearance of many of the characters with CIs of 1.00 is most likely the result of prevalent homoplasy that was calculated by PAUP. The ensemble homoplasy index was around 67%. This is the result of the sheer size of the data set, and could explain the lack of clear clusters along within any of the cladograms calculated.

CONCLUSIONS

Many characters were structured and coded based on the taxonomic work by Gorjunova (1985; 1992), and this dependence on her work allows a fair comparison between her taxonomy and a cladistic one. Comparing her 1992 taxonomy (Table 3) to the best tree produced by any of the cladistic software, especially Fig. 6, shows essentially no correlation between the two demonstrating that key-character taxonomy is not the same as that produced by cladistic software. Although a few of the families (Rhabdomesidae, Nikiforovellidae, and Streblotrypidae) and with some subfamilies

Fig 2: Q-mode analysis done in PAST based on Euclidean distance and Ward clustering.

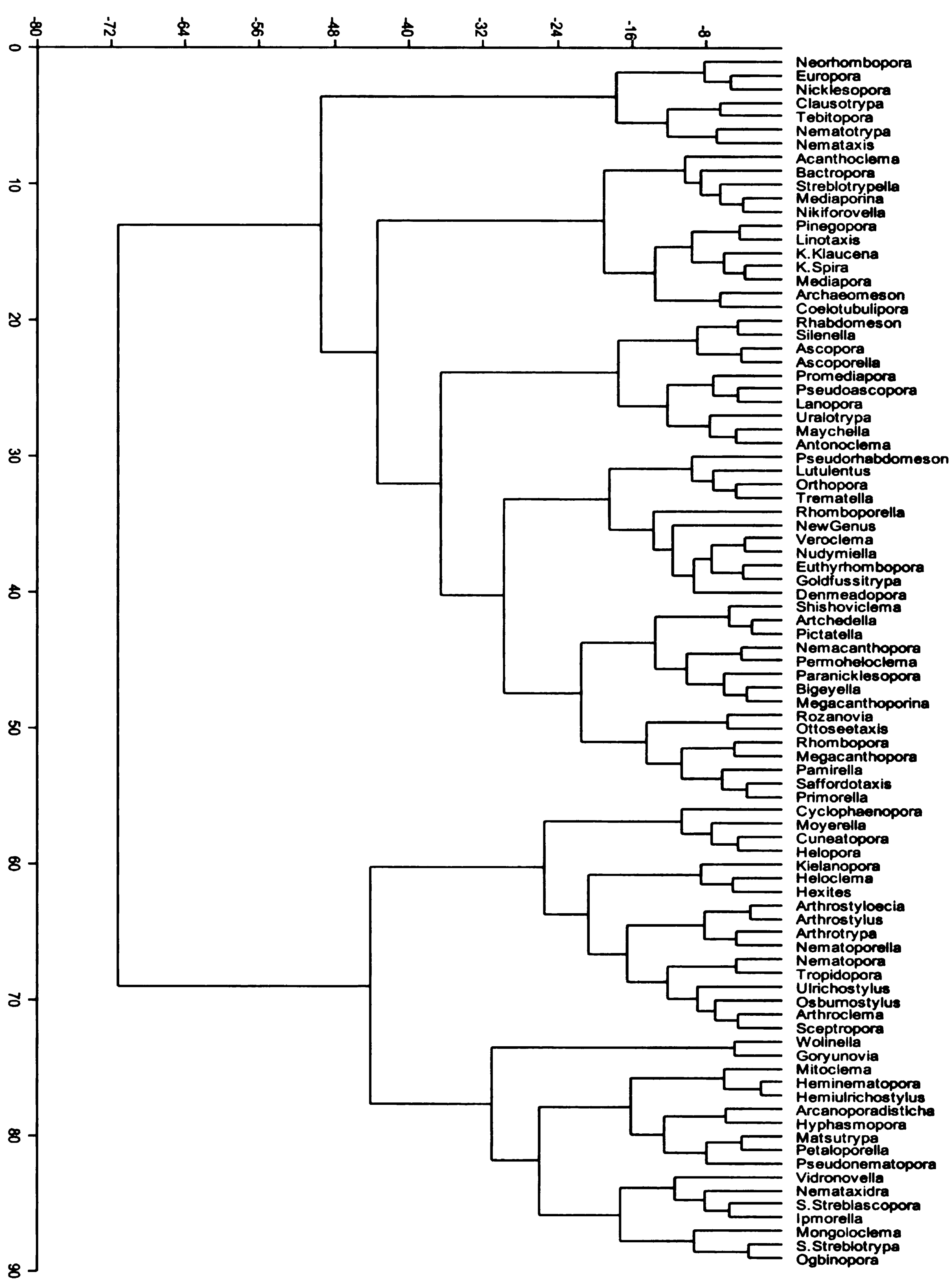

Fig 3: Strict consensus tree of the 12 MPTs calculated by PAUP

```
/-------------------------------------------------------- Wolinella
+-------------------------------------------------------- Goryunovia
|                                         /--- Cuneatopora
|                                        /91/-- Helopora
|                                       92 90-- Moyerella
|                                      /93\----- Osburnostylus
|                                     94 \------ Ulrichostylus
|             /---------------------------95\-------- Sceptropora
|             |                        \--------- Arthroclema
|             |                           /-- Nematotrypa
|             |                           96-- Cyclophaenopora
|             |                         /97--- Clausotrypa
|             |                        98----- Tebitopora
|             |                      /99------ Nemataxis
|             |                     100-------- Neorhombopora
|             |          /-------------102      /-- Europora
|             |          |              \----101-- Nicklesopora
|             |          |                   /-- Archaeomeson
|             |          |                   103-- Coelotubulipora
|             |          |                  104--- Mediaporina
|             |          |               /---105----- Promediapora
|             |          |               |      /-- Acanthoclema
|             |          |               |     106-- Nikiforovella
|             |          |               |    108/-- Bactropora
|             |          |               |  109107-- Streblotrypella
|             |          |              116    |\----- Pinegopora
|             |          |               || 111  /-- Pamirella
|             |          |               ||112 \-110-- Primorella
|             |          |               || |\-------- Linotaxis
|             |          |             117115     /-- K.Klaucena
|             |          |              | | |    113-- Mediapora
|             |          |            118 |  \---114--- K.Spira
|             |        140            | | \----------- Antonoclema
|             |        ||     120 \-------------- Nudymiella
|             |        ||     ||            /-- Veroclema
|             |        ||    121\-----------119-- Denmeadopora
|             |        ||    | \----------------- Maychella
|             |        ||  123              /-- NewGenus
|           157         ||  124\--------------122-- Uralotrypa
|           | |         || | \-------------------- Euthyrhombopora
|           | |         || |           /-------- Trematella
|           | |         || |           | /------ Rhomboporella
|           | |         || |          129 |  /-- Rhabdomeson
|           | |         ||137          |128 125-- Ascopora
176           | |        141| ||          | |126--- Silenella
|           | |        | || ||        | 127----- Pseudorhabdomeson
|           | |        | || ||        |  /----- Saffordotaxis
|           | |        | || |\----------136 132 /--- Artchedella
|           | |        | || |         | |131/-- Shishoviclema
|           | |        | |139          |133 130-- Pictatella
|           | |        | | |          || \------ Rhombopora
|           | |       144 | |          135    /-- Megacanthopora
|           | |       | | | |         \---134-- Lutulentus
```

Fig 3 cont:

```
|           | |       | | | |                /-- Bigeyella
|           | |       | | | \-----------------138-- Megacanthoporina
|          159 |        | | \------------------------ Goldfussitrypa
|          || |     146 |                    /-- Orthopora
|          || |      || |                 142-- Heloclema
|          || |      || \--------------------143--- Paranicklesopora
|          || |      ||                    /-- Nemacanthopora
|          || |     151\-----------------------145-- Permoheloclema
|          || |     | |                    /-- Ottoseetaxis
|          || |     | |                  /147-- Rozanovia
|          || |   152 |                   | /-- Pseudoascopora
|        160| |    || \---------------------150148-- Ascoporella
|        | || |  153|                   149--- Lanopora
|        | || |  | |\------------------------------- Kielanopora
|        | || | 154 \-------------------------------- Hexites
|        | || |155\---------------------------------- Tropidopora
|        | ||156 \----------------------------------- Nematopora
|        | ||  \------------------------------------- Nematoporella
|       164 ||                        /-- Arthrostyloecia
|       | | |\----------------------------------158-- Arthrostylus
|       | | \--------------------------------------- Arthrotrypa
|       | |                          /-- Heminematopora
|      165 |                          161-- Hemiulrichostylus
|       || |                       162--- Arcanopora
|      166| \---------------------------------163----- Hyphasmopora
|      | |\------------------------------------------ Mitoclema
|    168 \-------------------------------------------- Matsutrypa
|     ||                             /-- Mongoloclema
|     |\------------------------------------------167-- Pseudonematopora
|    171                               /-- S.Streblotrypa
|    | |                           169-- Ogbinopora
|  172 \------------------------------------------170--- S.Streblascopora
|  173\------------------------------------------------ Petaloporella
|174 \------------------------------------------------- Nemataxidra
175\---------------------------------------------------- Ipmorella
 \---------------------------------------------------- Vidronovella
```

Fig. 4: Minimum RC value tree calculated in PAUP and ladderized in TreeviewX.

```
/-------------------------------------------------------- Wolinella
+-------------------------------------------------------- Goryunovia
|                                     /--- Cuneatopora
|                                    /91/-- Helopora
|                                    92 90-- Moyerella
|                                   /93\----- Osburnostylus
|                                   94 \------ Ulrichostylus
|        /---------------------------95\-------- Sceptropora
|        |                          \--------- Arthroclema
|        |                             /-- Nematotrypa
|        |                              96-- Cyclophaenopora
|        |                            /97--- Clausotrypa
|        |                            98----- Tebitopora
|        |                           /99------ Nemataxis
|        |                          100-------- Neorhombopora
|        |      /-------------102     /-- Europora
|        |      |            \----101-- Nicklesopora
|        |      |                 /-- Archaeomeson
|        |      |                 103-- Coelotubulipora
|        |      |                104--- Mediaporina
|        |      |          /---105----- Promediapora
|        |      |          |    /-- Acanthoclema
|        |      |          |    106-- Nikiforovella
|        |      |          |   108/-- Bactropora
|        |      |          |  109107-- Streblotrypella
|        |      |         116   |\----- Pinegopora
|        |      |         ||  111  /-- Pamirella
|        |      |         ||112 \-110-- Primorella
|        |      |         || |\-------- Linotaxis
|        |      |        117115     /-- K.Klaucena
|        |      |        | | |    113-- Mediapora
|        |      |       118 | \---114--- K.Spira
|        |     140       | |\----------- Antonoclema
|        |     ||     120 \-------------- Nudymiella
|        |     ||     ||         /-- Veroclema
|        |     ||    121\-----------119-- Denmeadopora
|        |     ||    | \---------------- Maychella
|        |     ||   123           /-- NewGenus
|       157     ||  124\--------------122-- Uralotrypa
|       | |     || | \------------------- Euthyrhombopora
|       | |     || |          /-------- Trematella
|       | |     || |          | /------ Rhomboporella
|       | |     || |         129 |  /-- Rhabdomeson
|       | |     ||137          |128 125-- Ascopora
176      | |     141| ||        | |126--- Silenella
|       | |    | || ||        | 127----- Pseudorhabdomeson
|       | |    | || ||        |  /----- Saffordotaxis
|       | |    | || |\----------136 132 /--- Artchedella
|       | |    | || |         |  |131/-- Shishoviclema
```

Fig 4 cont:

```
|          | |       | |139         |133 130-- Pictatella
|          | |       | | |         || \------ Rhombopora
|          | |      144 | |         135    /-- Megacanthopora
|          | |      | | | |         \---134-- Lutulentus
|          | |      | | | |               /-- Bigeyella
|          | |      | | | \-----------------138-- Megacanthoporina
|         159 |       | | \------------------------- Goldfussitrypa
|         || |     146 |                    /-- Orthopora
|         || |     || |                   142-- Heloclema
|         || |     || \---------------------143--- Paranicklesopora
|         || |     ||                      /-- Nemacanthopora
|         || |    151\------------------------145-- Permoheloclema
|         || |    | |                      /-- Ottoseetaxis
|         || |    | |                     /147-- Rozanovia
|         || |   152 |                     | /-- Pseudoascopora
|        160| |   || \----------------------150148-- Ascoporella
|        | || |  153|                      149--- Lanopora
|        | || |  | |\-------------------------------- Kielanopora
|        | || | 154 \--------------------------------- Hexites
|        | || |155\---------------------------------- Tropidopora
|        | ||156 \------------------------------------ Nematopora
|        | ||  \------------------------------------- Nematoporella
|       164 ||                          /-- Arthrostyloecia
|       | | |\-----------------------------------158-- Arthrostylus
|       | | \---------------------------------------- Arthrotrypa
|       | |                            /-- Heminematopora
|      165 |                            161-- Hemiulrichostylus
|      || |                          162--- Arcanopora
|      166| \-----------------------------------163----- Hyphasmopora
|      | |\--------------------------------------------- Mitoclema
|     168 \----------------------------------------------- Matsutrypa
|     ||                               /-- Mongoloclema
|     |\-------------------------------------------167-- Pseudonematopora
|    171                                /-- S.Streblotrypa
|    | |                              169-- Ogbinopora
|   172 \-----------------------------------------170--- S.Streblascopora
|  173\---------------------------------------------------- Petaloporella
|174 \---------------------------------------------------- Nemataxidra
175\----------------------------------------------------- Ipmorella
 \------------------------------------------------------ Vidronovella
```

Fig 5: Minimum RI value tree calculated by PAUP and ladderized in TreeviewX.

```
/---------------------------------------------------------- Wolinella
+----------------------------------------------------------- Goryunovia
|                                      /--- Cuneatopora
|                                     /91/-- Helopora
|                                     92 90-- Moyerella
|                                    /93\----- Osburnostylus
|                                    94 \------ Ulrichostylus
|         /----------------------------95\-------- Sceptropora
|         |                         \--------- Arthroclema
|         |                              /-- Nematotrypa
|         |                               96-- Cyclophaenopora
|         |                             /97--- Clausotrypa
|         |                            98----- Tebitopora
|         |                           /99------ Nemataxis
|         |                          100-------- Neorhombopora
|         |       /-------------102     /-- Europora
|         |       |            \----101-- Nicklesopora
|         |       |                  /-- Archaeomeson
|         |       |                  103-- Coelotubulipora
|         |       |                 104--- Mediaporina
|         |       |              /---105----- Promediapora
|         |       |              |      /-- Acanthoclema
|         |       |              |     106-- Nikiforovella
|         |       |              |    108/-- Bactropora
|         |       |              |  109107-- Streblotrypella
|         |       |             116   |\----- Pinegopora
|         |       |             || 111  /-- Pamirella
|         |       |             ||112 \-110-- Primorella
|         |       |             || |\-------- Linotaxis
|         |       |            117115      /-- K.Klaucena
|         |       |            | |  |   113-- Mediapora
|         |       |          118 |  \---114--- K.Spira
|         |      140          | |\------------ Antonoclema
|         |      ||    120 \-------------- Nudymiella
|         |      ||    ||            /-- Veroclema
|         |      ||    121\-----------119-- Denmeadopora
|         |      ||    | \----------------- Maychella
|         |      ||   123            /-- NewGenus
|        157       || 124\--------------122-- Uralotrypa
|        | |       || | \-------------------- Euthyrhombopora
|        | |       || |          /-------- Trematella
|        | |       || |          | /------ Rhomboporella
|        | |       || |        129 | /-- Rhabdomeson
|        | |       ||137          |128 125-- Ascopora
176       | |        141| ||          | |126--- Silenella
|        | |       | || ||        | 127----- Pseudorhabdomeson
|        | |       | || ||        |  /----- Saffordotaxis
|        | |       | || |\----------136 132 /--- Artchedella
|        | |       | || |         | |131/-- Shishoviclema
```

Fig 5 cont:

```
|          | |       | |139          |133 130-- Pictatella
|          | |       | | |          || \------ Rhombopora
|          | |      144 | |          135   /-- Megacanthopora
|          | |      | | | |         \---134-- Lutulentus
|          | |      | | | |              /-- Bigeyella
|          | |      | | | \-----------------138-- Megacanthoporina
|         159 |      | | \------------------------- Goldfussitrypa
|          || |    146 |               /-- Orthopora
|          || |    || |             142-- Heloclema
|          || |    || \--------------------143--- Paranicklesopora
|          || |    ||                  /-- Nemacanthopora
|          || |   151\------------------------145-- Permoheloclema
|          || |   | |                /-- Ottoseetaxis
|          || |   | |               /147-- Rozanovia
|          || |  152 |               | /-- Pseudoascopora
|        160| |  || \---------------------150148-- Ascoporella
|         | || | 153|               149--- Lanopora
|         | || | | |\------------------------------ Kielanopora
|         | || | 154 \------------------------------- Hexites
|         | || |155\--------------------------------- Tropidopora
|         | ||156 \---------------------------------- Nematopora
|         | || \----------------------------------- Nematoporella
|        164 ||                        /-- Arthrostyloecia
|        | | |\-----------------------------------158-- Arthrostylus
|        | | \---------------------------------------- Arthrotrypa
|        | |                          /-- Heminematopora
|      165 |                          161-- Hemiulrichostylus
|      || |                         162--- Arcanopora
|     166| \---------------------------------163----- Hyphasmopora
|     | |\-------------------------------------------- Mitoclema
|    168 \---------------------------------------------- Matsutrypa
|     ||                              /-- Mongoloclema
|     |\------------------------------------------167-- Pseudonematopora
|   171                               /-- S.Streblotrypa
|   | |                             169-- Ogbinopora
|  172 \-------------------------------------------170--- S.Streblascopora
| 173\--------------------------------------------------- Petaloporella
|174 \--------------------------------------------------- Nemataxidra
175\----------------------------------------------------- Ipmorella
 \------------------------------------------------------- Vidronovella
```

Fig. 6: Minimum CI value tree calculated by PAUP and ladderized in TreeviewX.

```
/--------------------------------------------------------- Wolinella
+--------------------------------------------------------- Goryunovia
|                                        /--- Cuneatopora
|                                      /91/-- Helopora
|                                      92 90-- Moyerella
|                                    /93\----- Osburnostylus
|                                    94 \------ Ulrichostylus
|           /-----------------------------95\-------- Sceptropora
|           |                          \--------- Arthroclema
|           |                               /-- Nematotrypa
|           |                                96-- Cyclophaenopora
|           |                              /97--- Clausotrypa
|           |                              98----- Tebitopora
|           |                            /99------ Nemataxis
|           |                           100-------- Neorhombopora
|           |        /-------------102     /-- Europora
|           |        |             \----101-- Nicklesopora
|           |        |                     /-- Archaeomeson
|           |        |                     103-- Coelotubulipora
|           |        |                    104--- Mediaporina
|           |        |               /---105----- Promediapora
|           |        |               |       /-- Acanthoclema
|           |        |               |     106-- Nikiforovella
|           |        |               |    108/-- Bactropora
|           |        |               |  109107-- Streblotrypella
|           |        |              116   |\----- Pinegopora
|           |        |              ||  111   /-- Pamirella
|           |        |              ||112 \-110-- Primorella
|           |        |              || |\-------- Linotaxis
|           |        |             117115      /-- K.Klaucena
|           |        |             | | |    113-- Mediapora
|           |        |            118 |  \---114--- K.Spira
|           |       140         | | \------------ Antonoclema
|           |       ||      120 \-------------- Nudymiella
|           |       ||      ||          /-- Veroclema
|           |       ||     121\-----------119-- Denmeadopora
|           |       ||     | \----------------- Maychella
|           |       ||   123               /-- NewGenus
|          157       ||  124\--------------122-- Uralotrypa
|          ||       ||  | \------------------- Euthyrhombopora
|          ||       ||  |           /-------- Trematella
|          ||       ||  |           | /------ Rhomboporella
|          ||       ||  |          129 |  /-- Rhabdomeson
|          ||       ||137           |128 125-- Ascopora
176         ||       141| ||          |  |126--- Silenella
|          ||      | || ||          | 127----- Pseudorhabdomeson
|          ||      | || ||          |  /----- Saffordotaxis

|          ||      | || |\----------136 132 /--- Artchedella
|          ||      | || |           |  |131/-- Shishoviclema
```

Fig 6 cont:

```
|          | |        | |139         |133 130-- Pictatella
|          | |        | | |         || \------ Rhombopora
|          | |       144 | |         135   /-- Megacanthopora
|          | |       | | | |         \---134-- Lutulentus
|          | |       | | | |              /-- Bigeyella
|          | |       | | | \-----------------138-- Megacanthoporina
|         159 |       | | \------------------------- Goldfussitrypa
|         || |      146 |               /-- Orthopora
|         || |      || |             142-- Heloclema
|         || |      || \---------------------143--- Paranicklesopora
|         || |      ||                /-- Nemacanthopora
|         || |     151\-----------------------145-- Permoheloclema
|         || |     | |                /-- Ottoseetaxis
|         || |     | |               /147-- Rozanovia
|         || |    152 |               | /-- Pseudoascopora
|        160| |   || \---------------------150148-- Ascoporella
|        | || |  153|                149--- Lanopora
|        | || |  | |\------------------------------- Kielanopora
|        | || | 154 \-------------------------------- Hexites
|        | || |155\----------------------------------- Tropidopora
|        | ||156 \----------------------------------- Nematopora
|        | || \------------------------------------- Nematoporella
|       164 ||                        /-- Arthrostyloecia
|       | | |\----------------------------------158-- Arthrostylus
|       | | \---------------------------------------- Arthrotrypa
|       | |                           /-- Heminematopora
|      165 |                          161-- Hemiulrichostylus
|      || |                         162--- Arcanopora
|     166| \------------------------------------163----- Hyphasmopora
|     | |\-------------------------------------------- Mitoclema
|    168 \---------------------------------------------- Matsutrypa
|    ||                               /-- Mongoloclema
|    |\------------------------------------------167-- Pseudonematopora
|   171                                /-- S.Streblotrypa
|   | |                               169-- Ogbinopora
|  172 \------------------------------------------170--- S.Streblascopora
| 173\---------------------------------------------------- Petaloporella
|174 \---------------------------------------------------- Nemataxidra
175\------------------------------------------------------ Ipmorella
 \-------------------------------------------------------- Vidronovella
```

Table 3: List of node numbers at the bases of four prominent clades and corresponding characters at each node along with its equivalent CI value. Those listed are nodes that were present at clusters on the phylogram in Fig. 10.

```
            Branch                Character  Steps      CI   Change
-------------------------------------------------------------------
      node_157 --> node_95        4              1   0.231  2 ==> 1
                                  5              1   0.231  2 ==> 1
                                  66             1   0.111  2 ==> 3
                                  84             1   0.063  0 --> 1
                                  92             1   0.200  1 ==> 2
                                  129            1   0.077  1 ==> 2
                                  133            1   0.065  1 ==> 2
      node_140 --> node_102       108            1   0.333  0 ==> 1
                                  109            1   0.500  0 ==> 1
                                  117            1   1.000  0 ==> 1
                                  121            1   0.400  0 ==> 1
                                  122            1   1.000  0 ==> 1
                                  123            1   0.667  0 ==> 1
                                  124            3   0.444  0 ==> 3
                                  125            1   1.000  0 ==> 1
      node_157 --> node_156       4              1   0.231  2 --> 3
                                  12             1   0.429  2 ==> 1
                                  13             1   0.500  1 ==> 0
                                  14             1   0.333  2 ==> 1
                                  34             1   0.107  2 ==> 1
                                  88             1   0.111  2 --> 1
                                  144            1   0.071  1 ==> 2
                                  145            1   0.129  2 ==> 3
      node_176 --> node_175       1              3   1.000  0 ==> 3
                                  2              1   1.000  0 ==> 1
                                  3              3   0.375  0 ==> 3
                                  4              1   0.231  0 ==> 1
                                  5              1   0.231  0 ==> 1
                                  6              1   0.222  0 ==> 1
                                  7              3   0.250  0 ==> 3
                                  8              1   0.250  0 ==> 1
                                  11             1   1.000  1 ==> 2
                                  18             1   1.000  0 ==> 1
                                  28             1   0.077  0 ==> 1
                                  29             1   0.107  0 ==> 1
                                  31             2   0.107  0 ==> 2
                                  33             1   1.000  0 ==> 1
                                  35             3   0.182  0 ==> 3
                                  51             1   0.053  1 ==> 0
                                  72             1   0.286  0 ==> 1
                                  74             1   0.105  0 ==> 1
                                  75             1   0.500  0 ==> 1
                                  79             1   0.111  0 ==> 1
                                  80             2   0.083  0 ==> 2
                                  81             1   0.091  0 ==> 1
                                  82             1   0.222  0 ==> 1
                                  83             2   0.047  2 ==> 0
                                  87             1   0.500  1 ==> 2
                                  88             1   0.111  0 ==> 1
                                  94             1   0.154  0 ==> 1
```

Table 3 cont:

```
127                 1  0.286  0 ==> 1
128                 1  0.138  0 ==> 1
171                 3  0.125  0 ==> 3
```

(Saffordotaxinae and Nematotrypinae) clustered close to each other, the overall taxonomy proposed by Gorjunova (1985) is not supported cladistically.

Few other families fall into cladistic clusters. The cladistic analysis done in PAUP suggests a new taxonomy for the rhabdomesines (Table 10). Familial names were based on the the presence of the nominate genus within a given cluster for which the family is named. Other previous taxonomic studies and systematic listings (Blake 1983 and Bock 2007) show that the only family proposed in any of the three studies that displayed any consistent phenetic or cladistic structure was the Arthrostylidae, with the highest percent (50%) of genera supported in a cladistic cluster, yet this family was excluded from the order by Gorjunova for reasons yet to be determined.

Most likely it was due to the families' unilaminate characters that aren't found in almost all of the other genera coded in this study. This was taken from the minimum CI tree (Fig 6); however the PAST tree provided a more comprehensive cluster (comprising ~75%) of most of the arthrostylids. However, not all of the arthrostylids clustered together but were separated into four smaller clusters, and appear to be one of the lowest branching clades in the analysis.

Fig. 7: Strict consensus tree of the eight MPTs found using all the taxa coded.

```
/-------------------------------------------------------- Wolinella
+-------------------------------------------------------- Goryunovia
|                                     /--- Cuneatopora
|                                    /91/-- Helopora
|                                     92 90-- Moyerella
|                                    /93\----- Osburnostylus
|                                   94 \------ Ulrichostylus
|            /---------------------------95\-------- Sceptropora
|            |                      \--------- Arthroclema
|            |                         /-- Nematotrypa
|            |                          96-- Cyclophaenopora
|            |                        /97--- Clausotrypa
|            |                       98----- Tebitopora
|            |                      /99------ Nemataxis
|            |                     100-------- Neorhombopora
|            |         /-------------102    /-- Europora
|            |         |           \----101-- Nicklesopora
|            |         |               /-- Archaeomeson
|            |         |               103-- Coelotubulipora
|            |         |              104--- Mediaporina
|            |         |          /---105----- Promediapora
|            |         |          |     /-- Acanthoclema
|            |         |          |    106-- Nikiforovella
|            |         |          |   108/-- Bactropora
|            |         |          |  109107-- Streblotrypella
|            |         |         116   |\----- Pinegopora
|            |         |         || 111  /-- Pamirella
|            |         |         ||112 \-110-- Primorella
|            |         |         || |\-------- Linotaxis
|            |         |        117115    /-- K.Klaucena
|            |         |        | | |  113-- Mediapora
|            |         |       118 | \---114--- K.Spira
|            |        140       | | \------------ Antonoclema
|            |         ||    120 \-------------- Nudymiella
|            |         ||     ||          /-- Veroclema
|            |         ||    121\-----------119-- Denmeadopora
|            |         ||    | \----------------- Maychella
|            |         ||  123             /-- NewGenus
|           157          || 124\--------------122-- Uralotrypa
|           | |        || | \-------------------- Euthyrhombopora
|           | |        || |         /-------- Trematella
|           | |        || |         | /------ Rhomboporella
|           | |        || |       129 |  /-- Rhabdomeson
|           | |        ||137        |128 125-- Ascopora
176           | |       141| ||          | |126--- Silenella
|           | |       | || ||        | 127----- Pseudorhabdomeson
|           | |       | || ||        |  /----- Saffordotaxis
|           | |       | || |\----------136 132 /--- Artchedella
|           | |       | || |         |  |131/-- Shishoviclema
```

Fig 7 cont:

```
|         | |       | |139        |133 130-- Pictatella
|         | |       | | |        || \------ Rhombopora
|         | |      144 | |        135   /-- Megacanthopora
|         | |      | | | |       \---134-- Lutulentus
|         | |      | | | |              /-- Bigeyella
|         | |      | | | \-----------------138-- Megacanthoporina
|        159 |      | | \------------------------- Goldfussitrypa
|        || |    146 |                /-- Orthopora
|        || |    || |               142-- Heloclema
|        || |    || \---------------------143--- Paranicklesopora
|        || |    ||                 /-- Nemacanthopora
|        || |   151\-----------------------145-- Permoheloclema
|        || |    | |                /-- Ottoseetaxis
|        || |    | |               /147-- Rozanovia
|        || |  152 |                | /-- Pseudoascopora
|       160| |  || \---------------------150148-- Ascoporella
|       | || |  153|                149--- Lanopora
|       | || |  | |\------------------------------- Kielanopora
|       | || | 154 \--------------------------------- Hexites
|       | || |155\---------------------------------- Tropidopora
|       | ||156 \----------------------------------- Nematopora
|       | || \-------------------------------------- Nematoporella
|      164 ||                          /-- Arthrostyloecia
|      | | |\-----------------------------------158-- Arthrostylus
|      | | \---------------------------------------- Arthrotrypa
|      | |                           /-- Heminematopora
|     165 |                          161-- Hemiulrichostylus
|     || |                         162--- Arcanopora
|    166| \-----------------------------------163----- Hyphasmopora
|    | |\-------------------------------------------- Mitoclema
|   168 \---------------------------------------------- Matsutrypa
|    ||                              /-- Mongoloclema
|    |\------------------------------------------167-- Pseudonematopora
|  171                                /-- S.Streblotrypa
|  | |                              169-- Ogbinopora
| 172 \-----------------------------------------170--- S.Streblascopora
| 173\-------------------------------------------------- Petaloporella
|174 \-------------------------------------------------- Nemataxidra
175\---------------------------------------------------- Ipmorella
 \----------------------------------------------------- Vidronovella
```

Fig 8: Strict consensus tree of the three MPTs found with the minimum CI reweighting.

```
/----------------------------------------------------- Wolinella(1)
+----------------------------------------------------- Goryunovia(2)
|                                  /--- Cuneatopora(3)
|              /-----------100------------+ /- Helopora(22)
|              |                    100- Moyerella(25)
|              |                     /- Nematotrypa(4)
|              |                    100- Cyclophaenopora(21)
|              |                   100--- Clausotrypa(77)
|              |                  100---- Tebitopora(89)
|              |                 100------ Nemataxis(33)
|              |                100------- Neorhombopora(80)
|              |               100      /- Europora(37)
|              |               |\--100--+- Nicklesopora(55)
|              |              100  /------ Goldfussitrypa(20)
|              |              || |  /- Orthopora(31)
|              |              |\100+  100- Heloclema(57)
|              |              |   |100--- Paranicklesopora(60)
|              |             100    100 /- Nemacanthopora(53)
|              |             ||     100+- Permoheloclema(84)
|              |            100|       /- Bigeyella(41)
|              |            ||\---100----+- Megacanthoporina(61)
|              |            |\------------ Lutulentus(86)
|              |            |        /- Veroclema(23)
|              |            |        100- Denmeadopora(75)
|              |            |      100--- Nudymiella(65)
|              |            |     100 /- NewGenus(54)
|              |            100--100--+ 100+- Antonoclema(73)
|              |            ||     \------ Euthyrhombopora(38)
|              |            ||        /- Trematella(32)
|              |            | +----100-----+- Rhomboporella(62)
|              |            ||        /- Artchedella(66)
|             100           100 |        +- Rhombopora(70)
|             ||           || \----100-----+- Shishoviclema(72)
|             ||           ||        \- Pictatella(81)
|             ||           ||        /- Uralotrypa(76)
|             ||           |\-----100------+- Maychella(87)
|             ||          100          /- Rhabdomeson(64)
|             ||          ||        100- Ascopora(68)
|             ||          ||       100--- Silenella(79)
|             ||         100 |      100---- Pseudorhabdomeson(69)
|             ||         || \---100----+------ Ascoporella(74)
|             ||        100\------------------- Lanopora(67)
|             ||       100 \------------------- Pseudoascopora(44)
|             ||      100\--------------------- Promediapora(43)
|             ||      | \---------------------- Mediaporina(29)
|             ||  100               /- Ottoseetaxis(11)
|            100|  |\---------100----------+- Rozanovia(42)
|            | ||  100         /--------- Archaeomeson(6)
|            | ||  ||          | /------- Linotaxis(40)
```

Fig 8 cont:

```
|            | ||  | \------100-------+ |    /- K.Klaucena(49)
|            | ||  |                  | |/100-+- Mediapora(52)
|            | ||  |                  100+------ K.Spira(50)
|            | || 100                    ||   /- Saffordotaxis(51)
|            | || ||                   100  100- Megacanthopora(71)
|            | || ||                    |100--- Primorella(88)
|          100 ||  ||                     100---- Pamirella(78)
|           || ||100|                     \------ Pinegopora(85)
|           || || ||\--------------------------- Bactropora(35)
|           || |100|                     /- Acanthoclema(30)
|           || |  |\-----------100-----------+- Nikiforovella(47)
|           || |  \------------------------------ Streblotrypella(48)
|          100| \-------------------------------- Osburnostylus(10)
|          | ||                      /- Arthroclema(15)
|          | ||                      100- Sceptropora(16)
|          | |\-------------100-------------+--- Ulrichostylus(17)
|         100 |                        /- Arthrostyloecia(7)
|          || \--------------100---------------+- Arthrostylus(14)
|          ||                        /- Kielanopora(5)
|         100\---------------100----------------+- Hexites(58)
|         | |                        /--- Nematoporella(19)
|        100 \---------------100---------------+ /- Nematopora(24)
|        ||                          100- Tropidopora(34)
|       100\---------------------------------------- Arthrotrypa(18)
|       ||                           /- Arcanopora(28)
|       100\-----------------100------------------+- Hyphasmopora(56)
|       | \----------------------------------------- Matsutrypa(26)
|      100                            /- Heminematopora(8)
|      ||                            100- Hemiulrichostylus(9)
|     67+\------------------100------------------+--- Mitoclema(13)
|     | |                            /- Mongoloclema(27)
|     | \--------------------67--------------------+- Pseudonematopora(59)
|    67                               /- S.Streblotrypa(63)
|    ||                              100- Ogbinopora(83)
|  100\-------------------100--------------------+--- S.Streblascopora(82)
| 100 \--------------------------------------------- Petaloporella(39)
|  |\---------------------------------------------- Nemataxidra(12)
|100                                 /- Coelotubulipora(36)
100\----------------------100----------------------+- Ipmorella(45)
 \-------------------------------------------------- Vidronovella(46)
```

Fig 9: Phylogram created in PAUP with labeled nodes and OTUs. Phylogram could not be output into any other software to expand the compressed format.

```
/-- Wolinella
+------- Goryunovia
|                             /- Cuneatopora
|                            91/--- Helopora
|                           9290---- Moyerella
|                          93\--- Osburnostylus
|                         94\--- Ulrichostylus
|                         95-- Sceptropora
|                         |\-- Arthroclema
|                         |                       /---------- Nematotrypa
|                         |                     /96--------- Cyclophaenopora
|                         |                   /97------ Clausotrypa
|                         |                  98------- Tebitopora
|                         |                /99---- Nemataxis
|                         |             /100-- Neorhombopora
|                         |        /--102    /-- Europora
|                         |        |    \--101--- Nicklesopora
|                         |        |     /--- Archaeomeson
|                         |        |   103---- Coelotubulipora
|                         |        | 104- Mediaporina
|                         |        | 105-- Promediapora
|                         |        |  |    /---- Acanthoclema
|                         |        |  |  106- Nikiforovella
|                         |        |  |108/---- Bactropora
|                         |        |  10107--- Streblotrypella
|                         |        |116 +--- Pinegopora
|                         |        |  111/-- Pamirella
|                         |        | 11110- Primorella
|                         |        |  |+-- Linotaxis
|                         |        |1115/--- K.Klaucena
|                         |        | |113- Mediapora
|                         |        11114- K.Spira
|                         |      140 |\- Antonoclema
|                         |       |120-- Nudymiella
|                         |       ||||/ Veroclema
|                         |       12119---- Denmeadopora
|                         |       ||+--- Maychella
|                         |       123 /--- NewGenus
|                       157       12122-- Uralotrypa
|                        ||       ||+- Euthyrhombopora
|                        ||       ||+-- Trematella
|                        ||       ||+------ Rhomboporella
|                        ||       129   /- Rhabdomeson
|                        ||       128 125-- Ascopora
176                      ||     141||126-- Silenella
|                        ||      |||127------- Pseudorhabdomeson
|                        ||      ||||/-- Saffordotaxis
|                        ||      |1132/ Artchedella
|                        ||      |||131--- Shishoviclema
|                        ||      131130-- Pictatella
|                        ||      ||||\-- Rhombopora
|                        ||    144135 /--- Megacanthopora
|                        ||      |||134--- Lutulentus
|                        ||      |||/-- Bigeyella
|                        ||      |138- Megacanthoporina
|                      159|      |\- Goldfussitrypa
|                      | ||    146 /- Orthopora
|                      | ||     |142--- Heloclema
|                      | ||     143-- Paranicklesopora
```

Fig 9 cont:

```
|                     | ||     ||/-- Nemacanthopora
|                     | ||   15145- Permoheloclema
|                     | ||    ||   /------- Ottoseetaxis
|                     | ||    ||/147-- Rozanovia
|                     | ||  152||/- Pseudoascopora
|                   160 ||   |1148--- Ascoporella
|                   | | || 153149-- Lanopora
|                   | | ||  ||\---- Kielanopora
|                   | | ||154\---- Hexites
|                   | | |155\-- Tropidopora
|                   | | 156\--- Nematopora
|                   | | | \--- Nematoporella
|                 164 | | /-- Arthrostyloecia
|                  || | 158- Arthrostylus
|                  || \-- Arthrotrypa
|                  ||   / Heminematopora
|                165| 161- Hemiulrichostylus
|                  |162------ Arcanopora
|                1163---- Hyphasmopora
|                | +--- Mitoclema
|              168 \- Matsutrypa
|                | /-------- Mongoloclema
|                167--- Pseudonematopora
|              171 /-- S.Streblotrypa
|                169-- Ogbinopora
|              1170-- S.Streblascopora
|             173\- Petaloporella
|            174\-- Nemataxidra
\----------175 \--- Ipmorella
             \------- Vidronovella
```

Fig 10: Cladogram created in PAUP based on reweighting of characters by the minimum CI value with labeled nodes and OTUs.

```
/------------------------------------------------------------ Wolinella
+------------------------------------------------------------ Goryunovia
|                                                        /--- Cuneatopora
|                                                      /91/-- Helopora
|                                                     92 90-- Moyerella
|                                                   /93\----- Osburnostylus
|                                                  94 \------ Ulrichostylus
|                   /-----------------------------95\-------- Sceptropora
|                   |                              \--------- Arthroclema
|                   |                                     /-- Nematotrypa
|                   |                                    96-- Cyclophaenopora
|                   |                                  /97--- Clausotrypa
|                   |                                 98----- Tebitopora
|                   |                               /99------ Nemataxis
|                   |                             100-------- Neorhombopora
|                   |              /-------------102      /-- Europora
|                   |              |               \----101-- Nicklesopora
|                   |              |                      /-- Archaeomeson
|                   |              |                    103-- Coelotubulipora
|                   |              |                   104--- Mediaporina
|                   |              |             /---105----- Promediapora
|                   |              |             |        /-- Acanthoclema
|                   |              |             |      106-- Nikiforovella
|                   |              |             |     108/-- Bactropora
```

Fig 10 cont:

```
|                  |              |             |   109107-- Streblotrypella
|                  |              |           116    |\----- Pinegopora
|                  |              |            ||  111   /-- Pamirella
|                  |              |            ||112 \-110-- Primorella
|                  |              |            || |\-------- Linotaxis
|                  |              |          117115      /-- K.Klaucena
|                  |              |          | |  |    113-- Mediapora
|                  |              |        118 |  \---114--- K.Spira
|                  |            140        | | \------------ Antonoclema
|                  |             ||      120 \-------------- Nudymiella
|                  |             ||       ||             /-- Veroclema
|                  |             ||     121\-----------119-- Denmeadopora
|                  |             ||     | \----------------- Maychella
|                  |             ||   123                /-- NewGenus
|                157             ||  124\--------------122-- Uralotrypa
|                | |             ||  | \-------------------- Euthyrhombopora
|                | |             ||  |             /-------- Trematella
|                | |             ||  |             | /------ Rhomboporella
|                | |             ||  |           129 |   /-- Rhabdomeson
|                | |             ||137            |128 125-- Ascopora
176              | |           141| ||            |  |126--- Silenella
|                | |           | || ||            | 127----- Pseudorhabdomeson
|                | |           | || ||            |   /----- Saffordotaxis
|                | |           | || |\----------136 132 /--- Artchedella
|                | |           | || |             |  |131/-- Shishoviclema
|                | |           | |139             |133 130-- Pictatella
|                | |           | |  |             || \------ Rhombopora
|                | |         144 |  |            135     /-- Megacanthopora
|                | |         | | |  |              \---134-- Lutulentus
|                | |         | | |  |                    /-- Bigeyella
|                | |         | | |  \------------------138-- Megacanthoporina
|              159 |         | | \-------------------------- Goldfussitrypa
|               || |       146 |                         /-- Orthopora
|               || |        || |                       142-- Heloclema
|               || |        || \----------------------143--- Paranicklesopora
|               || |        ||                           /-- Nemacanthopora
|               || |      151\-------------------------145-- Permoheloclema
|               || |      | |                            /-- Ottoseetaxis
|               || |      | |                         /147-- Rozanovia
|               || |    152 |                         |  /-- Pseudoascopora
|             160| |     || \-----------------------150148-- Ascoporella
|             | || |   153|                           149--- Lanopora
|             | || |   | |\--------------------------------- Kielanopora
|             | || | 154 \---------------------------------- Hexites
|             | || |155\------------------------------------ Tropidopora
|             | ||156 \------------------------------------- Nematopora
|             | ||  \--------------------------------------- Nematoporella
|           164 ||                                       /-- Arthrostyloecia
|           | | |\-------------------------------------158-- Arthrostylus
|           | | \------------------------------------------- Arthrotrypa
|           | |                                          /-- Heminematopora
|         165 |                                        161-- Hemiulrichostylus
|          || |                                       162--- Arcanopora
|        166| \-------------------------------------163----- Hyphasmopora
|        | |\----------------------------------------------- Mitoclema
|      168 \------------------------------------------------ Matsutrypa
|       ||                                               /-- Mongoloclema
|       |\---------------------------------------------167-- Pseudonematopora
|     171                                                /-- S.Streblotrypa
|     | |                                              169-- Ogbinopora
|   172 \---------------------------------------------170--- S.Streblascopora
```

Fig 10 cont:

```
|  173\---------------------------------------------------- Petaloporella
|174 \----------------------------------------------------- Nemataxidra
175\------------------------------------------------------- Ipmorella
  \-------------------------------------------------------- Vidronovella
```

Table 4: List of node numbers at the base of significant clades and corresponding characters at each node along with its equivalent CI value. Those listed are nodes that were present at clusters on the cladogram in Fig. 13. Only the first node duplicates change present in Table 8.

```
                 Branch                  Character  Steps      CI   Change
--------------------------------------------------------------------------
       node_157 --> node_95              4              1   0.231   2 ==> 1
                                         5              1   0.231   2 ==> 1
                                         66             1   0.111   2 ==> 3
                                         84             1   0.063   0 --> 1
                                         92             1   0.200   1 ==> 2
                                         129            1   0.077   1 ==> 2
                                         133            1   0.065   1 ==> 2
       node_102 --> node_100             41             1   0.053   2 --> 1
                                         44             1   0.087   1 --> 0
                                         45             1   0.077   1 --> 0
                                         50             1   0.094   3 ==> 2
                                         80             1   0.083   1 ==> 2
                                         110            1   0.222   0 --> 1
                                         118            1   0.500   0 ==> 1
                                         120            1   0.667   0 ==> 1
                                         121            1   0.400   1 --> 2
                                         123            1   0.667   1 ==> 2
                                         151            1   0.105   0 ==> 1
       node_102 --> node_101             28             2   0.077   0 ==> 2
                                         43             1   0.065   1 --> 2
                                         51             1   0.053   0 ==> 1
                                         79             1   0.111   2 ==> 1
                                         113            1   1.000   0 ==> 1
                                         114            1   0.500   0 ==> 1
                                         115            2   0.500   0 ==> 2
                                         117            1   1.000   1 ==> 2
                                         124            1   0.444   3 --> 4
                                         126            2   0.065   2 ==> 0
                                         129            1   0.077   1 --> 2
                                         183            1   0.091   0 ==> 1
       node_116 --> node_105             131            2   0.067   2 ==> 0
                                         132            1   0.133   1 ==> 0
                                         148            1   0.095   1 ==> 0
                                         150            1   0.167   1 ==> 0
                                         151            1   0.105   1 ==> 0
                                         157            1   0.133   1 ==> 0
       node_115 --> node_112             31             1   0.107   3 --> 2
                                         60             1   0.143   2 ==> 1
                                         61             1   0.115   3 ==> 2
                                         74             1   0.105   1 --> 2
```

Table 4 cont:

```
                                  84              2  0.063  0 ==> 2
                                  130             1  0.091  1 ==> 2
                                  146             1  0.081  2 ==> 1
       node_128 --> node_127      9               1  0.250  0 ==> 1
                                  10              1  0.400  0 ==> 1
                                  62              1  0.066  4 ==> 3
                                  80              1  0.083  1 ==> 2
                                  129             1  0.077  1 ==> 2
                                  130             1  0.091  1 --> 2
                                  145             1  0.129  4 ==> 3
                                  148             1  0.095  1 --> 0
                                  181             3  0.079  0 ==> 3
       node_135 --> node_133      43              1  0.065  2 --> 1
                                  50              1  0.094  3 --> 2
                                  80              1  0.083  1 --> 2
                                  131             2  0.067  2 ==> 0
                                  132             1  0.133  1 ==> 0
                                  172             1  0.100  2 --> 3
                                  174             1  0.091  0 --> 1
       node_151 --> node_150      28              1  0.077  0 ==> 1
                                  80              1  0.083  2 --> 1
                                  81              1  0.091  2 --> 1
                                  83              1  0.047  1 ==> 0
                                  181             1  0.079  0 ==> 1
       node_164 --> node_163      59              1  0.059  1 --> 0
                                  74              1  0.105  1 ==> 2
       node_171 --> node_170      28              1  0.077  1 ==> 2
                                  29              2  0.107  1 ==> 3
                                  42              1  0.111  0 ==> 1
                                  59              1  0.059  1 --> 2
                                  78              3  0.138  0 ==> 3
                                  80              1  0.083  2 --> 1
                                  104             3  0.070  0 --> 3
                                  181             2  0.079  1 ==> 3
```

In the PAUP tree, the Family Rhabdomesidae, although historically composed of the most genera, was broken into many small clusters towards the top of the tree, intermixed with supposed rhomboporids and nikiforovellids. The PAST tree actually provided a better clustering of this group (60%) but it was not as clustered together as that of the arthrostylids. The Hyphasmoporidae are another example of a well clustered family with at least 50% present in clusters in both the PAUP and PAST trees. The phenetic method, although providing better clustering of the OTUs, rather than a more pectinate structure, did not provide percentages of genera in conventional families as high as either of the two cladistic methods. These two examples support the hypothesis that the amount of homoplasy in each analysis increased going from the PAUP analysis, then to the PAST, and finally to the phenetic analysis. It is proposed here that all previous or existing rhabdomesine taxonomies should be thoroughly reworked. Most previous taxonomies relied on morphological similarities and did not result from of cladistic analyses. The results of the phenetic output (Fig. 2) show even less similarity to previous taxonomies (Gorjunova 1985, Blake 1983, and Bock 2007). Therefore the phenetic result is the least acceptable conclusion for this study.

The resulting support of clusters in the PAUP tree at their bases appears to be quite low, with a very small number of clusters containing characters with high CIs (around 1.00) at the base of their node (Table 8). The only cluster that appears to be supported by at least one character with a CI of 1.00 is node 102 (Table 8) containing the conventional families Nicklesoporidae and Nematotrypidae. The other nodes listed in Table 8 show the bases of clusters, but these nodes do not contain characters with significant CIs, except for node 175, which is a pectinate cluster of some of the Streblotrypidae. Fig. 11 and Table 9 show support for clusters in the minimum CI tree (ladderized version in Fig. 8). Again, looking at the table, there is not much support by characters with high CIs at any of the nodes at cluster points. This also tends to show that support for a large number of genera within a particular family, especially within the arthrostylids or the rhabdomesids, is almost certainly impossible, and perhaps it makes more sense to divide these taxa into smaller subfamilies like those of Gorjunova (1992) than to lump them into large families (like those of Blake 1983 and Bock 2007).

It appears that there is no clear correlation between the stratigraphic ages of the genera and the cladistic output. It is just as likely to find both young and older taxa throughout the branch order of the tree, even when starting at the base. The nominate genus of each family as proposed in the conventional taxonomy tends to show that the lower, or oldest, family is the hyphasmoporids, followed by the arthrostylids, rhabdomesids, rhomboporids, and at the very top of the tree are the bactroporids (which includes the nikiforovellids). However, using Fig. 8 to establish the familial ordering of the tree, it shows that the oldest family is the Streblotrypidae which, based on its oldest genus, is much younger than any of the arthrostlyids, Upper Mississippian in age compared to most arthrostylids which are Mid-Late Ordovician. Therefore, stratigraphic ages that were used for the order of input in the data matrix used in all of the cladistic and phenetic analyses seem to have no bearing on the topology of each cladogram. Using another option instead of the AS-IS option for input of OTUs may alter the outcome of the trees created in each of the programs.

The presence of the genera in Table 6 in the consensus cladogram in Fig. 11 suggests a possible placement of *Hayasakapora* (a presumed girtyporid), *Kielcepora,* and *Ojlepora* (both kielceporids) within the Family Arthroclemidae, and therefore in the Suborder Nikiforovellina (Gorjunova 1992). *Idioclema* and *Hyalotoechus* (putative trepostomes) also clustered with an undescribed genus that was used in the study embedded in the tree, possibly suggesting a close familial relationship among the three. The other three genera (*Maychellina* (maychellinid), *Pesnastylus* (phylloporinid?), and *Syringoclemis* (girtyporid)) were embedded in the tree, with *Maychellina* appearing within the Nematotrypidae, *Pesnastylus* within a grouping of arthrostylids, and

Syringoclemis appearing towards the base of the tree in a small cluster with *Coelotubulipora* and *Archaeomeson.* This could mean that these genera are correctly placed in the Rhabdomesidae or that there are some convergences between the morphologies of the rhabdomesines and other orders such as the trepostomes that affect the structure of the cladogram.

Finally, considering at the genera of uncertain affinities, there doesn't seem to be any significant difference if the genera of uncertain affinity are added to the tree (Fig 8). However, it does reduce the amount of pectinate structure, mostly in the consensus tree rather than the individual MPTs themselves. The three presumed encrusters (*Streblocladia, Rhombocladia,* and *Strebloplax*) to appear at the bottom of the cladogram, because the encrusting growth form causes them to lose most of the branching characters (Appendix A), which are crucial for the rhabdomesines. This could lead one to hypothesize that the encrusting forms of these genera reflect an artificially primitive placement within the tree. Their position is most likely an artifact of their lack of diagnostic character states.

Table 5: Alternative classification of the Suborder Rhabdomesina based on the cladogram in Fig. 8. Familial placement based on clusters within the tree, starting from the root of the tree. Genera left out of any of the families listed below were because they were singletons (showing no internal relationships within the tree) or doubletons, therefore placement in any of the families lacked any evidence.

Order Cryptostomida
  Suborder Rhabdomesina
    Family Streblotrypidae
      Streblotrypa
      Streblascopora
      Ogbinopora
    Family Hyphasmoporidae
      Hyphasmopora
      Arcanopora
      Hemiulrichostylus

Table 5 cont:

- *Heminematopora*
- **Family Arthrostylidae**
  - *Arthrostylus*
  - *Arthrostyloecia*
- **Family 1**
  - *Arthroclema*
  - *Sceptropora*
  - *Ulrichostylus*
  - *Osburnostylus*
  - *Cuneatopora*
  - *Moyerella*
  - *Helopora*
- **Family Pseudoascoporidae**
  - *Pseudoascopora*
  - *Rozanovia*
  - *Ottoseetaxis*
  - *Lanopora*
  - *Ascoporella*
- **Family 2**
  - *Paranicklesopora*
  - *Heloclema*
  - *Orthopora*
- **Family Nicklesoporidae**
  - *Nicklesopora*
  - *Europora*
- **Family Nematotrypidae**
  - *Nematotrypa*
  - *Neorhombopora*
  - *Nemataxis*
  - *Tebitopora*
  - *Clausotrypa*
  - *Cyclophaenopora*
- **Family Rhabdomesidae**
  - *Rhabdomeson*
  - *Trematella*
  - *Rhomboporella*
  - *Pseudorhabdomeson*
  - *Silenella*
  - *Ascopora*
- **Family Rhomboporidae**
  - *Rhombopora*
  - *Lutulentus*
  - *Megacanthopora*
  - *Saffordotaxis*
  - *Artchedella*
  - *Pictatella*
  - *Shishoviclema*
- **Family 3**
  - *Promediapora*
  - *Mediaporina*
  - *Coelotubulipora*
  - *Archaeomeson*
- **Family Mediaporidae**
  - *Mediapora*
  - *Klaucena (Spira)*

Table 5 cont:

- *Klaucena (Klaucena)*
- **Family Bactroporidae**
  - *Bactropora*
  - *Pinegopora*
  - *Streblotrypella*
  - *Nikiforovella*
  - *Acanthoclema*

APPENDIX A

APPENDIX A

Table 6: Taxonomy of the Suborder Rhabdomesina adapted from Blake (1983). The nominate genus of each family is listed first, with remaining genera listed in alphabetical order.

- **Order Cryptostomata**
  - **Suborder Rhabdomesina**
    - **Family Arthrostylidae**
      - *Arthrostylus*
      - *Arthroclema*
      - *Arthrostyloecia*
      - *Cuneatopora*
      - *Arcanopora*
      - *Heloclema*
      - *Helopora*
      - *Heminematopora*
      - *Hemiulrichostylus*
      - *Hexites*
      - *Moyerella*
      - *Nematopora*
      - *Osburnostylus*
      - *Pseudonematopora*
      - *Sceptropora*
      - *Tropidopora*
      - *Ulrichostylus*
    - **Family Rhabdomesidae**
      - *Rhabdomeson*
      - *Ascopora*
      - *Mediapora*
      - *Nemataxis*
      - *Nicklesopora*
      - *Orthopora*
      - *Trematella*
    - **Family Rhomboporidae**
      - *Rhombopora*
      - *Klaucena (Klaucena)*
      - *Klaucena (Spira)*
      - *Megacanthopora*
      - *Pamirella*
      - *Primorella*
      - *Saffordotaxis*
    - **Family Bactroporidae**
      - *Bactropora*
    - **Family Nikiforovellidae**
      - *Nikiforovella*

Table 6 cont:

- *Acanthoclema*

- *Pinegopora*
- *Streblotrypella*

Family Hyphasmoporidae

- *Hyphasmopora*
- *Ogbinopora*
- *Streblotrypa*
- *Streblascopora*

Family Uncertain

- *Petaloporella*

Genera not included by Blake (1983)

- *Archaeomeson*
- *Clausotrypa*
- *Denmeadopora*
- *Hayasakapora*
- *Hyalotoechus*
- *Idioclema*
- *Linotaxis*
- *Maychella*
- *Mongoloclema*
- *Nemacanthopora*
- *Nemataxidra*
- *Nematotrypa*
- *Ottoseetaxis*
- *Pesnastylus*
- *Rhombocladia*
- *Rhomboporella*
- *Syringoclemis*

APPENDIX B

APPENDIX B

Table 7: Taxonomy of the Order Rhabdomesida adapted from Gorjunova 1985. Unplaced genera within the rhabdomesids not listed.

- **Phyllum Bryozoa**
  - **Class Stenolaemata**
    - **Order Rhabdomesida**
      - **Suborder Goldfussitrypina**
        - **Family Goldfussitrypidae**
          - **Subfamily Goldfussitrypinae**
            - *Goldfussitrypa*
            - *Verella (*now *Veroclema)*
          - **Subfamily Nicklesoporinae**
            - *Nicklesopora*
        - **Family Mediaporidae**
            - *Mediapora*
        - **Family Maychellinidae**
            - *Maychellina*
        - **Family Maychellidae**
            - *Maychella*
      - **Suborder Streblotrypina**
        - **Family Nematoporidae**
          - **Subfamily Nematoporinae**
            - *Nematopora*
            - *Arthroclema*
            - *Cuneatopora*
            - *Ottoseetaxis*
          - **Subfamily Primorellinae**
            - *Nemataxis*
            - *Hexites*
          - *Primorella*
          - **Subfamily Helocleminae**
            - *Heloclema*
            - *Permoheloclema*
        - **Family Nematotrypidae**
          - **Subfamily Nematotrypinae**
            - *Nematotyrpa*
            - *Pseudonematopora*
            - *Nemacanthopora*
            - *Clausotrypa*
          - **Subfamily Moyerellinae**
            - *Moyerella*
        - **Family Streblotrypidae**
          - **Subfamily Heloporinae**
            - *Helopora*

Table 7 cont:

- *Sceptropora*
- *Neorhombopora*
- **Subfamily Streblotrypina**
  - *Matsutrypa*
  - *Petaloporella*
  - *Streblotrypa*
- **Family Rhomboporidae**
  - **Subfamily Saffordotaxinae**
    - *Orthopora*
    - *Acanthoclema*
    - *Saffordotaxis*
    - *Klaucena*
    - *Pamirella*
  - **Subfamily Rhomboporinae**
    - *Rhombopora*
    - *Linotaxis*
    - *Shishoviclema*
- **Family Nikiforovellidae**
  - *Nikiforovella*
  - *Artchedella*
  - *Pinegopora*
- **Family Nudymiellidae**
  - *Nudymiellidae*
- **Suborder Rhabdomesina**
  - **Family Pseudoascoporidae**
    - *Pseudoascopora*
  - **Family Streblascoporidae**
    - *Ipmorella*
    - *Streblascopora*
    - *Lanopora*
    - *Ogbinopora*
  - **Family Rhabdomesidae**
    - *Rhabdomeson*
    - *Ascopora*

APPENDIX C

APPENDIX C

Table 8: Taxonomy of the Order Rhabdomesida from Gorjunova (1992). Unplaced genera within the rhabdomesids not listed.

- **Class Stenolaemata**
  - **Order Rhabdomesida**
    - **Suborder Goldfussitrypina**
      - **Family Goldfussitrypidae**
        - **Subfamily Goldfussitrypinae**
          - *Goldfussitrypa*
          - *Veroclema*
        - **Subfamily Nicklesoporinae**
          - *Paranicklesopora*
          - *Nicklesopora*
      - **Family Mediaporidae**
        - *Mediapora*
        - *Promediapora*
      - **Family Maychellidae**
        - *Maychella*
    - **Suborder Nikiforovellina**
      - **Family Arthroclemidae**
        - **Subfamily Arthrocleminae**
          - *Nematopora*
          - *Cuneatopora*
          - *Ottoseetaxis*
          - *Arthroclema*
        - **Subfamily Primorellinae**
          - *Mitoclema*
          - *Nemataxis*
          - *Hexites*
          - *Primorella*
        - **Subfamily Helocleminae**
          - *Heloclema*
          - *Permoheloclema*
      - **Family Bactroporidae**
        - *Bactropora*
      - **Family Nematotrypidae**
      - **Subfamily Nematotrypinae**
          - *Nematotrypa*
          - *Clausotrypa*
          - *Nemacanthopora*
          - *Pseudonematopora*
        - **Subfamily Moyerellinae**
          - *Moyerella*
          - *Helopora*

Table 8 cont:

- **Family Hyphasmoporidae**
  - **Subfamily Sceptroporinae**
    - *Sceptropora*
    - *Trematella*
    - *Neorhombopora*
  - **Subfamily Hyphasmoporinae**
    - *Matsutrypa*
    - *Petaloporella*
    - *Rozanovia*
    - *Hyphasmopora*
- **Family Rhomboporidae**
  - **Subfamily Saffordotaxinae**
    - *Orthopora*
    - *Saffordotaxis*
    - *Klaucena*
    - *Pamirella*
  - **Subfamily Rhomboporinae**
    - *Rhombopora*
    - *Linotaxis*
    - *Shishoviclema*
- **Family Nikiforovellidae**
    - *Acanthoclema*
    - *Nikiforovella*
    - *Streblotrypella*
    - *Artchedella*
    - *Pinegopora*
- **Family Nudymiellidae**
    - *Nudymiella*

Suborder Rhabdomesina

- **Family Pseudoascoporidae**
    - *Pseudoascopora*
    - *Silenella*
- **Family Streblotrypidae**
    - *Ipmorella*
    - *Streblotrypa*
    - *Lanopora*
    - *Streblascopora*
    - *Ogbinopora*
- **Family Rhabdomesidae**
    - *Rhabdomeson*
    - *Ascopora*
    - *Ascoporella*

APPENDIX D

APPENDIX D

Table 9: Bock's (2007) systematic listing of the Order Cryptostomida using family nomenclature from Blake (1983) and Taylor (1993). Nomenclature of other suborders and families added from Gorjunova (1985).

- **Order Cryptostomida**
  - **Suborder Rhabdomesina**
    - **Family Arthrostylidae**
      - *Arthrostylus*
      - *Arcanopora*
      - *Arthroclema*
      - *Arthrostyloecia*
      - *Arthrotrypa*
      - *Cuneatopora*
      - *Cyclophaenopora*
      - *Helopora*
      - *Heminematopora*
      - *Hemiulrichostylus*
      - *Hexites*
      - *Matsutrypa*
      - *Moyerella*
      - *Nematopora*
      - *Nematoporella*
      - *Osburnostylus*
      - *Ottoseetaxis*
      - *Permoheloclema*
      - *Pseudonematopora*
      - *Sceptropora*
      - *Tropidopora*
      - *Ulrichostylus*
      - *Veroclema*
    - **Family Rhabdomesidae**
      - *Rhabdomeson*
      - *Archaeomeson*
      - *Ascopora*
      - *Bigeyella*
      - *Coelotubulipora*
      - *Denmeadopora*
      - *Euthyrhombopora*
      - *Heloclema*
      - *Lutulentus*
      - *Mediaporina*
      - *Megacanthopora*
      - *Nemacanthoclema*
      - *Nemataxidra*

Table 9 cont:

- *Nemataxis*
- *Neorhombopora*
- *Orthopora*
- *Pamirella*
- *Primorella*
- *Promediapora*
- *Pseudorhabdomeson*
- *Rhomboporella*
- *Spirillopora*
- *Streblocladia*
- *Strebloplax*
- *Trematella*
- *Uralotrypa*

Family Rhomboporidae

- *Rhombopora*
- *Klaucena (Klaucena)*
- *Linotaxis*
- *Megacanthoporina*
- *Pictatella*
- *Saffordotaxis*
- *Shishoviclema*
- *Klaucena (Spira)*

Family Bactroporidae

- *Bactropora*

Family Nikiforovellidae

- *Nikiforovella*
- *Artchedella*
- *Clausotrypa*
- *Pinegopora*
- *Robinella*
- *Streblotrypella*
- *Tebitopora*

Family Pseudoascoporidae

- *Pseudoascopora*
- *Silenella*

Family Hyphasmoporidae

- *Hyphasmopora*
- *Acanthoclema*
- *Ascoporella*
- *Ipmorella*
- *Mongoloclema*
- *Ogbinopora*
- *Rozanovia*
- *Streblotrypa*

Family Streblascoporidae

Table 9 cont:

- *Streblascopora*
- **Suborder Goldfussitrypina**
  - **Family Goldfussitrypidae**
    - *Goldfussitrypa*
    - *Nemacanthopora*
    - *Paranicklesopora*
  - **Family Maychellidae**
    - *Maychella*
  - **Family Mediaporidae**
    - *Mediapora*
  - **Family Nicklesoporidae**
    - *Nicklesopora*
    - *Europora*
  - **Family Vidronovellidae**
    - *Vidronovella*
- **Suborder Streblotrypina**
  - **Family Streblotrypidae**
    - *Streblotrypa*
  - **Family Nudymiellidae**
    - *Nudymiella*
  - **Family Nematoporidae**
    - *Nematopora*
  - **Family Nematotrypidae**
    - *Nematotrypa*
    - *Moyerella*
    - *Kielanopora*

APPENDIX E

APPENDIX E

Table 10: Stratigraphic ages of all genera in the study based on the International Commission on Stratigraphy (ICS) (stratigraphy.org, 2008). "Unspecified" indicates unknown stage therefore the absolute midpoint of the epoch/stage was used as the best estimate. The genera listed are in stratigraphic order.

Genus Name	**Stage**	**Series/System**	**FAD (MA)**
Goryunovia	Floian	Lower Ordovician	478.6
Wolinella	Dapingian	Middle Ordovician	471.8
Cuneatopora	Darriwilian	Middle Ordovician	468.1
Nematotrypa	Darriwilian	Middle Ordovician	468.1
Kielanopora	Darriwilian	Middle Ordovician	468.1
Kielcepora	Darriwilian	Middle Ordovician	468.1
Ojlepora	Darriwilian	Middle Ordovician	468.1
Archaeomeson	Unspecified	Middle Ordovician	466.35
Arthrostyloecia	Sandbian	Upper Ordovician	460.9
Heminematopora	Sandbian	Upper Ordovician	460.9
Hemiulrichostylus	Sandbian	Upper Ordovician	460.9
Osburnostylus	Sandbian	Upper Ordovician	460.9
Ottoseetaxis	Sandbian	Upper Ordovician	460.9
Nemataxidra	Sandbian	Upper Ordovician	460.9
Mitoclema	Sandbian	Upper Ordovician	460.9
Arthrostylus	Katian	Upper Ordovician	455.8
Arthroclema	Katian	Upper Ordovician	455.8
Sceptropora	Katian	Upper Ordovician	455.8
Ulrichostylus	Katian	Upper Ordovician	455.8
Arthrotrypa	Katian	Upper Ordovician	455.8
Nematoporella	Katian	Upper Ordovician	455.8
Goldfussitrypa	Katian	Upper Ordovician	455.8
Cyclophaenopora	Sandbian/Katian	Upper Ordovician	453.25
Arcanopora	Hirnantian	Upper Ordovician	445.6
Helopora	Telychian	Llandovery Silurian	436
Nematopora	Telychian	Llandovery Silurian	436
Veroclema	Telychian	Llandovery Silurian	436
Moyerella	Unspecified	Llandovery Silurian	435.95
Matsutrypa	Unspecified	Llandovery Silurian	435.95
Mongoloclema	Unspecified	Llandovery Silurian	435.95
Arcanopora	Unspecified	Wenlock Silurian	425.25
Pesnastylus	Ludfordian	Ludlow Silurian	421.3

Table 10 cont:

Mediaporina	Pridoli	Pridoli Silurian	418.7
Acanthoclema	Lochkovian	Lower Devonian	416
Nemataxis	Lochkovian	Lower Devonian	416
Orthopora	Lochkovian	Lower Devonian	416
Trematella	Lochkovian	Lower Devonian	416
Tropidopora	Lochkovian	Lower Devonian	416
Bactropora	Givetian	Middle Devonian	391.8
Coelotubulipora	Givetian	Middle Devonian	391.8
Europora	Givetian	Middle Devonian	391.8
Euthyrhombopora	Givetian	Middle Devonian	391.8
Petaloporella	Unspecified	Middle Devonian	391.4
Linotaxis	Frasnian	Upper Devonian	385.3
Hyalotoechus	Frasnian	Upper Devonian	385.3
Bigeyella	Frasnian	Upper Devonian	385.3
Rozanovia	Frasnian	Upper Devonian	385.3
Promediapora	Frasnian	Upper Devonian	385.3
Pseudoascopora	Famennian	Upper Devonian	374.5
Ipmorella	Famennian	Upper Devonian	374.5
Vidronovella	Famennian	Upper Devonian	374.5
Nikiforovella	Tournaisian	Lower Mississippian	359.2
Streblotrypella	Tournaisian	Lower Mississippian	359.2
K. Klaucena	Tournaisian	Lower Mississippian	359.2
K. Spira	Tournaisian	Lower Mississippian	359.2
Saffordotaxis	Tournaisian	Lower Mississippian	359.2
Mediapora	Tournaisian	Lower Mississippian	359.2
Nicklesopora	Tournaisian	Lower Mississippian	359.2
Nemacanthopora	Tournaisian	Lower Mississippian	359.2
New Genus	Tournaisian	Lower Mississippian	359.2
Hyphasmopora	Visean	Middle Mississippian	345.3
Heloclema	Visean	Middle Mississippian	345.3
Hexites	Visean	Middle Mississippian	345.3
Pseudonematopora	Visean	Middle Mississippian	345.3
Hayasakapora	Visean	Middle Mississippian	345.3
Paranicklesopora	Visean	Middle Mississippian	345.3
Megacanthoporina	Visean	Middle Mississippian	345.3
Rhomboporella	Unspecified	Carboniferous	329.1

Table 10 cont:

Genus Name	**Stage**	**Series/System**	**FAD (MA)**
Strebloplax	Serpukhovian	Upper Mississippian	328.3
Syringoclemis	Serpukhovian	Upper Mississippian	328.3
Nudymiella	Unspecified	Middle Carboniferous	317.75
Artchedella	Unspecified	Middle Carboniferous	317.75
Maychellina	Unspecified	Mid-Upper Carboniferous	313.65
Lanopora	Bashkirian/Moscovian	Lower-Middle Pennsylvaniar	312.65
Ascopora	Moscovian	Middle Pennsylvanian	311.7
Rhombocladia	Kasimovian	Upper Pennsylvanian	307.2
Pseudorhabdomeson	Kasimovian	Upper Pennsylvanian	307.2
Rhombopora	Gzhelian	Upper Pennsylvanian	303.4
Megacanthopora	Gzhelian	Upper Pennsylvanian	303.4
Shishoviclema	Gzhelian	Upper Pennsylvanian	303.4
Antonoclema	Gzhelian	Upper Pennsylvanian	303.4
Ascoporella	Sakmarian	Cisuralian Permian	294.6
Streblocladia	Sakmarian	Cisuralian Permian	294.6
Denmeadopora	Sakmarian	Cisuralian Permian	294.6
Uralotrypa	Sakmarian/Artinskian	Cisuralian Permian	285.1
Clausotrypa	Unspecified	Lower Permian	284.8
Pamirella	Artinskian	Cisuralian Permian	284.4
Silenella	Artinskian	Cisuralian Permian	284.4
Neorhombopora	Artinskian	Cisuralian Permian	284.4
Pictatella	Kungurian	Cisuralian Permian	275.6
S. Streblascopora	Unspecified	Permian	275
Ogbinopora	Roadian	Guadalupian Permian	270.6
Permoheloclema	Roadian	Guadalupian Permian	270.6
Pinegopora	Wordian	Guadalupian Permian	268
Lutulentus	Wordian	Guadalupian Permian	268
Maychella	Unspecified	Guadalupian Permian	265.5
Primorella	Unspecified	Upper Permian	258.4
Tebitopora	Ladinian	Middle Triassic	237

WORKS CITED

WORKS CITED

Anstey, R. L. & Perry, T. G., 1970. Biometric procedures in taxonomic studies of Paleozoic bryozoans. *Journal of Paleontology* 44: 383-398.

Anstey, R. L. & Perry, T. G., 1973. Eden Shale bryozoans: a numerical study (Ordovician, Ohio Valley). *Mich State Univ Publ Mus Paleontol Ser* 1: 1-80.

Anstey, R. L., 1978. Taxonomic survivorship and morphologic complexity in Paleozoic bryozoan genera. *Paleobiology* 4 (4): 407-418.

Anstey, R. 1990. Bryozoans. p. 232-252. In K. Mcnamara (ed.), Evolutionary trends. Belhaven Press, London.

Anstey, R. and Pachut, J. 1995. Phylogeny, diversity history, and speciation in Paleozoic bryozoans. p. 239-284. In D. Erwin, and R. Anstey (eds.), New approaches to speciation in the fossil record. Columbia University Press, New York.

Blake, D. 1980. Homeomorphy in Paleozoic bryzoans: a search for explanations. Paleobiology 6: 451-465.

Blake, D. 1983a. Introduction to the Suborder Rhabdomesina. P. 530-592. In R. Robinson (ed.), Treatise on invertebrate paleontology part G, Bryozoa (revised) Geological Society of America, Inc. and The University of Kansas, Boulder and Lawrence.

Blake, D. 1983b. The Order Cryptostomata, p. 440-452. In R. Robinson (ed.), Treatise on invertebrate paleontology part G, Bryozoa (revised). Geological Society of America, Inc. and The University of Kansas, Boulder and Lawrence.

Blake, D. and Snyder, E. 1987. Phenetic and cladistic analyses of the Rhabdomesina (Bryozoa) and similar taxa: a preliminary study. P. 33-40. In J. Ross (ed.), Bryozoa: Past and Present. Western Washington University, Bellingham.

Corneliussen, E.F. & Perry, T.G., 1973. *Monotrypa*, *Hallopora*, *Amplexopora*, and *Hennigopora* (Ectoprocta) from the Brownsport Formation (Niagaran), Western Tennessee. *Journal of Paleontology* 47 (2): 151-220.

Cuffey, R. 1973. An improved classification, based upon numerical-taxonomic analyses, for the higher taxa of Entoproct and Ectoproct bryozoans. p. 549-564. In G. Larwood (ed.), Living and fossil Bryozoa. Academic Press, New York.

Cuffey, R. and Blake, D. 1991. Cladistic analysis of the Phylum Bryozoa. P. 97-108. In P. Bigey (ed.), Bryozoa living and fossil. Bull. Soc. Sci. Nat. Ouest Fr., Mem. HS 1.

Dzik, Jerzy, 1981. Evolutionary relationships of the Early Paleozoic cyclostomatous Bryozoa. *Palaeontology*, 24: 827-862.

Dzik, J. 1992. Early astogeny and relationships of the Ordovician rhabdomesine bryozoans. Acta Palaeontologica Polonica 37: 37-54.

Dzik, J. 1994. Bryozoa of the Mojcza Limestone. Palaeontologica Polonica 53: 253-282.

Gilmour, E. H. 2007. New Carboniferous Bryozoa of the Bird Spring Formation, southern Nevada. *Journal of Paleontology* 81 (3): 581-587.

Gorjunova, R. V. & Morozova, I. P., 1979.Late Palaeozoic Bryozoa of Mongolia [in Russian]. *Sovmestnaya Sovetsko-Mongolskaya Paleontologischeskaya Ekspeditsiya Trudy* 9: 1-133. [New Species of Fossil Invertebrates from Mongolia: Proceedings of the Joint Soviet-Mongolian Paleontological Expedition].

Gorjunova, R. V., 1985. The morphology, systematics and phylogeny of Bryozoa (Order Rhabdomesida) [in Russian]. *Trudy Paleontologischeskogo Instituta Akademiya Nauk SSSR* 208: 1-152.

Gorjunova, R.V., 1992. [in Russian] Morphology and system of the Paleozoic bryozoans. *Trudy Paleontologischeskogo Instituta Akademiya Nauk SSSR*, 251: 1-168.

Hageman, S.J., 1991. Approaches to systematic and evolutionary studies of perplexing groups: an example using fenestrate Bryozoa. *Journal of Paleontology*, 65: 630-647.

Hammer, O. and Harper, D. 2007. PAST v. 1.74. University of Oslo.

Hickey, David R., 1988. Bryozoan astogeny and evolutionary novelties: their role in the origin and systematics of the Ordovician monticuliporid trepostome genus *Peronopora*. *Journal of Paleontology*, 62: 180-203.

Key, M.M.Jr, 1990. Intracolony variation in skeletal growth rates in Paleozoic ramose trepostome bryozoans. *Paleobiology*, 16: 483-491.

Mayr, E. and Ashlock, P. 1991. Principles of systematic zoology. McGraw-Hill, inc. NY.

McKinney, F. K., 1977. Autozooecial budding patterns in dendroid Paleozoic bryozoans. *Journal of Paleontology* 51: 303-329.

McKinney, Frank K., 2000. Phylloporinids and the phylogeny of the Fenestrida. In: *Proceedings of the 11th International Bryozoology Association Conference* (Herrera Cubilla, Amalia & Jackson, Jeremy B.C., editors), Smithsonian Tropical Research Institute, Balboa, R.P, pp. 54-65.

Morozova, I.P., 1992. [in Russian] Admiratellidae, a new family of the bryozoan order Fenestellida. *Paleontologicheskii Zhurnal*, 1992 (3): 3-8.

Morozova, I. P., 2003. New genus *Robinella* (Bryozoa) from the Lower Permian of eastern Australia [in Russian]. In: *Mshanki Zhyemnogo Shara (Bryozoa)* Vol. 1: 16-19. Izhd-vo KusGPA (Kuzbass Pedagogical Academy), Novokuznetsk.

Morozova, I. P., Weiss, O. B. & Racki, G., 2006. New Devonian and Carboniferous Bryozoans of the Holy Cross Mountains (Central Poland) [in Russian]. *Paleontologicheskii Zhurnal* 2006 (5): 58-67. (Also in Paleontological Journal; 40 (5):529-540).

Ozhgibesov, V.P., 1983. *Permoheloclema* - a new bryozoan genus of the Order Rhabdomesonida. *Paleontologicheskii Zhurnal*, 1983 (4): 96-98.

Pachut, J.F., & Anstey, R.L., 1984. The relative information content of Fourier-structural, binary (presence-absence) and combined data sets: a test using the H.A. Nicholson collection of Paleozoic stenolaemate bryozoans. *Journal of Paleontology*, 58: 1296-1311.

Pachut, J.F., Anstey, R.L., & Horowitz, A.S., 1994. The H.A Nicholson collection of Paleozoic stenolaemate bryozoans: comparison of cladistic and phenetic classifications. *Journal of Paleontology*, 68: 978-994.

Prezbindowski, Dennis R. & Anstey, Robert L., 1978. A Fourier-numerical study of a bryozoan fauna from the Threeforks Formation (Late Devonian) of Montana. *Journal of Paleontology* 52: 353-369.

Pushkin, V.I., 1990. [in Russian] Bryozoa of the family Ceramoporidae of Ordovician from the eastern European platform. In: New representatives of the fossil fauna and flora of Belorussia and other regions of the USSR: collected scientific papers: 5-34. Nauka y Tekhnika, Minsk.

Snell, Joanna F., 2004. Bryozoa from the Much Wenlock Limestone (Silurian) Formation of the West Midlands and Welsh Borderland. *Monograph of the Palaeontographical Society (London)* 157 (621): 1-136.

Spearing, K. 1998. Phylogenetic Analysis of the Rhabdomesine Bryozoans. Master's Thesis. Michigan State University.

Swofford, D. 2007. Phylogenetic Analysis Using Parsimony, v. 4.0. Smithsonian Institution, Washington, DC.

Tang, Su & Cuffey, Roger J., 1998. *Inconobotopora lichenoporoides* a new genus and species of cystoporate bryozoan from the Silurian of Gotland, and its evolutionary implication. *Journal of Paleontology* 72(2): 256-264.

Taylor, P.D., & Rozhnov, S., 1996. A new early cyclostome bryozoan from the Lower Ordovician (Volkhov Stage) of Russia. *Paläontologisches Zeitschrift*, 70: 171-180.

Taylor, P.D., & Weedon, M.J., 2000. Skeletal ultrastructure and phylogeny of cyclostome bryozoans. *Zoological Journal of the Linnean Society*, 128: 337-399.

Yang Jing-zhi, Hu Zhao-xun, & Xia Feng-sheng, 1988. Bryozoans from Late Devonian and Early Carboniferous of central Hunan. *Palaeontologica Sinica*, 174, New Series B,23: 1-198.

LIST OF REFERENCES

LIST OF REFERENCES

Bassler, R. S., 1929. The Permian Bryozoa of Timor. *Paläont. Timor* Lief. 16: 37-90.

Bassler, R. S., 1936. Nomenclatorial notes on fossil and Recent Bryozoa. *Journal of the Washington Academy of Science* 26: 156-162.

Bassler, R. S., 1952. Taxonomic notes on genera of fossil and Recent Bryozoa. *Journal of the Washington Academy of Science* 42: 381-385.

Bassler, R. S., 1953. *Bryozoa* Vol. Part G. pp.1-253. (Moore, Raymond C. Treatise on Invertebrate Paleontology) Geological Society of America and University of Kansas Press, Lawrence, Kansas.

Blake, D. 1983a. Introduction to the Suborder Rhabdomesina. P. 530-592. In R. Robinson (ed.), Treatise on invertebrate paleontology part G, Bryozoa (revised) Geological Society of America, Inc. and The University of Kansas, Boulder and Lawrence.

Blake, D. 1983b. The Order Cryptostomata, p. 440-452. In R. Robinson (ed.), Treatise on invertebrate paleontology part G, Bryozoa (revised). Geological Society of America, Inc. and The University of Kansas, Boulder and Lawrence.

Crockford, J. M., 1941. Permian Bryozoa from Eastern Australia, Part II: New species from the Upper Marine Series of New South Wales. *Journal of the Royal Society of New South Wales* 74: 502-519.

Crockford, J. M., 1944. Bryozoa from the Permian of Western Australia, Part I: Cyclostomata and Cryptostomata from the North-West Basin and the Kimberley District. *Proceedings of the Linnean Society of New South Wales* 69: 139-175.

Dzik, J. 1981. Evolutionary relationships of the Early Paleozoic cyclostomatous Bryozoa. *Palaeontology*, 24: 827-862.

Dzik, J. 1992. Early astogeny and relationships of the Ordovician rhabdomesine bryozoans. Acta Palaeontologica Polonica 37: 37-54.

Dzik, J. 1994. Bryozoa of the Mojcza Limestone. Palaeontologica Polonica 53: 253-282.

Fleming, P. J. G., 1969. Fossils from the Neerkol Formation in Central Queensland. In: Campbell, K.S.W. (editor) *Stratigraphy and Palaeontology: Essays in honour of Dorothy Hill*: 264-275. Australian National University Press, Canberra.

Gilmour, Ernest H., 2007. New Carboniferous Bryozoa of the Bird Spring Formation, southern Nevada. *Journal of Paleontology* 81 (3): 581-587.

Gorjunova, R. V., 1985. The morphology, systematics and phylogeny of Bryozoa (Order Rhabdomesida) [in Russian]. *Trudy Paleontologischeskogo Instituta Akademiya Nauk SSSR* 208: 1-152.

Gorjunova, R.V., 1992. [in Russian] Morphology and system of the Paleozoic bryozoans. *Trudy Paleontologischeskogo Instituta Akademiya Nauk SSSR*, 251: 1-168.

Gorjunova, R. V., 2002. *Pseudorhabdomeson* - A new genus of Carboniferous bryozoans: Morphology and astogeny. [in Russian] *Paleontologicheskii Zhurnal* 2002 (5): 49-58.

Hu, Zhao-xun, 1986. Late Ordovician bryozoans from Yushan County, Jiangxi Province. *Acta Micropalaeontologica Sinica* 3: 167-184.

Karklins, O. L., 1986. Chesterian (Late Mississipian) bryozoans from the upper Chainman Shale and the lowermost Ely Limestone of western Utah. *Memoir of the paleontological society* 17: 1-48.

Lisitsyn, D.V., 1991. [in Russian] New bryozoans from the Permian of northern Cisuralia. *Paleontologicheskii Zhurnal*, 1991 (4): 69-76.

Lobdell, Frederick K., 1992. Arthrostylidae (Bryozoa: Cryptostomata) from the Gunn Member, Stony Mountain Formation (Upper Ordovician), North Dakota and Manitoba. *North Dakota Geological Survey Miscellaneous Series*, 76: 99-115.

McNair, A. H., 1942. Upper Devonian Bryozoa. *Journal of Paleontology* 16: 343-350.

Morozova, I. P., 1970. Mshanki pozdney Permi (Late Permian bryozoans). *Trudy Paleontologischeskogo Instituta Akademiya Nauk SSSR* 122: 1-347. (?1-374).

Morozova, I. P. & Kruchinina, O. N., 1986. *Permian Bryozoa of the Arctic region [in Russian] (Permskie mshanki arktiki)*. 143. Akad. Nauk SSSR, Moscow.

Morozova, I. P., 2003. New genus *Robinella* (Bryozoa) from the Lower Permian of eastern Australia [in Russian]. In: *Mshanki Zhyemnogo Shara (Bryozoa)* Vol. 1: 16-19. Izhd-vo KusGPA (Kuzbass Pedagogical Academy), Novokuznetsk.

Morozova, I. P., Weiss, O. B. & Racki, G., 2006. New Devonian and Carboniferous Bryozoans of the Holy Cross Mountains (Central Poland) [in Russian]. *Paleontologicheskii Zhurnal* 2006 (5): 58-67. (Also in Paleontological Journal; 40 (5):529-540).

Shishova, N. A., 1965. The systematic position and size of the family Hyphasmoporidae [in Russian]. *Paleontologicheskii Zhurnal* 1965 (2): 55-62.

Spjeldnaes, Nils, 1984. Upper Ordovician bryozoans from Ojl Myr, Gotland, Sweden. *Bulletin of the Geological Institutions of the University of Uppsala, N.S.*, 10: 1-66.

Taylor, P.D., & Rozhnov, S., 1996. A new early cyclostome bryozoan from the Lower Ordovician (Volkhov Stage) of Russia.
Paläontologisches Zeitschrift, 70: 171-180.

Ulrich, E.O. 1882. American Paleozoic Bryozoa. Cincinnati Soc. Nat. History, v. 5, p. 121-175, pls. 6-8, p. 232-257, pls. 10, 11.

Ulrich, E.O. 1890. Geology and Paleontology. Geological Survey of Illinois. Legislature of Illinois. V. VIII.

Yang Jing-zhi, Hu Zhao-xun, & Xia Feng-sheng, 1988. Bryozoans from Late Devonian and Early Carboniferous of central Hunan. *Palaeontologica Sinica*, 174, New Series B,23: 1-198.